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Systematic revision of the genus Sorghastrum (Poaceae: Andropogoneae)

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Systematic revision of the genus Sorghastrum

(Poaceae: Andropogoneae)

by

Patricia Dolores Davila

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DEDICATION

To my parents, Rodolfo and Concepcion

I. INTRODUCTION

The main objectives of this dissertation are to define the genus Sorghastrum as compared with other related genera within the subfamily Andropogoneae, to systematically revise all the species belonging to this genus, and to define their relationships. This research is primarily based on gross morphology studies, chromosome counts, anatomical studies (leaf cross sections and epidermis), and a cladistic analysis. The revision of the genus includes keys, descriptions, references and citation of specimens.

The genus Sorghastrum belongs to the advanced and widespread grass subfamily Andropogoneae. The Andropogoneae includes about 85 genera and about 960 species (Clayton and Renvoize, 1986). These grasses are distributed throughout the tropics, particularly in savanna regions, and extend into the temperate zone. The major distinguishing characteristics of this subfamily are the spikelets with rigid elongate equal glumes and the arrangement of the spikelets in pairs, almost always borne upon a fragile rachis. This means that the function of dispersal is transferred from individual spikelets to the rachis segment (internode + 2 spikelets) (Clayton, 1972). There is also a general tendency towards reduction of the inflorescence and proliferation of axillary branches.

The probable center of origin of the Andropogoneae is the Indo-Malaysian region (Hartley, 1958), where the tribe is most abundant and has the most primitive taxa. In the Americas, taxa of this subfamily are less numerous, probably due to the fact that the Andropogoneae has not reached its full potential development (diversification and radiation

processes) in this region (Hartley, 1958). In general terms, there is little difficulty in defining or recognizing the boundaries of the Andropogoneae; on the other hand, it is more difficult to define generic limits. This is due to great morphological modification of the pedicelled spikelet and consequent reduction in inflorescence branches.

The genus Sorghastrum represents one of these taxonomic units that has had an uncertain systematic position because of the reduction of the pedicelled spikelet. According to Keng (1939), Sorghastrum represents one of the few Andropogoneae genera extending from Africa to tropical America. It was first proposed by Nash (1901), as a segregate genus from Sorghum. The only difference pointed out was the absence of a spikelet on the pedicel in Sorghastrum.

This work is the first attempt to carry out a monograph of the genus Sorghastrum in the world. Except for the information included in different Floras dealing only with local species, there is no comprehensive taxonomic treatment of Sorghastrum.

The number of species attributed to this genus has been quite variable throughout its history. Hitchcock (1930) and Keng (1939) included 10 species in Sorghastrum. Correll and Johnston in 1970 included 12 species in the genus. On the other hand, Swallen (1955), Gould (1968), Celarier (1959), as well as Hall (1982) proposed about 15 species comprising Sorghastrum. Clayton and Renvoize (1986) stated 16 species, whereas Burkart (1969) and Jacques-Felix (1962) suggested that the genus included 20 species. An extensive synonymy exists, including

about 100 names.

My studies indicate that Sorghastrum comprises 17 species inhabiting the New World and Africa. Eight species are South American (S. minarum, S. balansae, S. contractum, S. chaseae, S. pellitum, S. viride, S. scaberrimum, and S. stipoides). Two species are African (S. rigidifolium and S. trichopus). Two species are present in Mexico, Central America and South America (S. incompletum and S. setosum. One species (S. brunneum) occurs in Mexico and Central America. Finally, four species are North American (S. elliottii, S. secundum, S. nudipes, and S. nutans).

The altitudinal range of the genus varies greatly, from sea level to approximately 3000 m. Sorghastrum species are important elements of primary and secondary grasslands, as well as the edges of pine forests or scrub-like vegetation. There is a great variation among Sorghastrum species in their soil preference. S. elliottii is abundant in sandy woodlands (Correll and Johnston, 1970). Some others, such as S. incompletum, prefer open rocky hills or savannas (Hitchcock, 1913), but S. setosum is always associated with marshes or very wet places.

Many Sorghastrum species are forage grasses. Some species as S. nutans are considered most desirable forage grasses (Correll and Johnston, 1970). Others, such as S. pellitum, are considered to be low productive forages (Rosengurtt et al., 1970).

From anatomical and morphological studies I conclude that Sorghastrum is a well defined taxonomic entity, apart from Sorghum, Andropogon, Bothriochloa and other genera.

Comparative data on Sorghastrum species and related genera are

presented in chapters three through six. Each of these chapters contain a review of previous work and/or some original observations, and a discussion of possible interpretations of the data. Chapter eight presents leaf cross sections and epidermal descriptions of Sorghastrum and the 17 species. These descriptions are entirely the result of the anatomical work carried out in this dissertation. Chapter nine contains revised taxonomic descriptions of Sorghastrum and each recognized species. In chapter ten, a summary of this study and its contribution to the systematics of Sorghastrum is presented.

II. MATERIALS AND METHODS

A. Herbarium Studies

Herbarium specimens were examined to determine distribution, phenology, and morphological variation. Listed below, using standard abbreviations from Holmgren et al. (1981), are the herbaria from which loan material was obtained.

A - Arnold Arboretum of Harvard University, Cambridge, Massachusetts

B - Botanischer Garten und Botanisches Museum Berlin- Dahlem

BAB - Instituto Nacional de Tecnologia Agropecuaria, Buenos Aires, Argentina

BR - Jardin Botanique National de Belgique, Meise, Belgium

C - Botanical Museum and Herbarium, Copenhagen, Denmark

CHAPA - Herbario-Hortorio, Rama de Botanica, Colegio de Postgraduados Chapingo, Mexico

CETES - Instituto de Botanica del Nordeste, Corrientes, Argentina

COT - Herbario de la Comision Tecnica Consultiva para la determinacion de indices de agostadero, Mexico

F - Field Museum, Chicago, Illinois

FLAS - University of Florida, Gainesville

G - Conservatoire et Jardin Botaniques de la Ville de Geneve, Switzerland

GH - Gray Herbarium of Harvard University, Cambridge, Massachusetts

ISC - Iowa State University, Ames

K - Royal Botanical Gardens, Kew, England

LE - Komarov Botanical Institute of the Academy of Sciences of the U.S.S.R., Leningrad

LP - Division Plantas Vasculares del Museo de la Plata, Buenos Aires, Argentina

MO - Missouri Botanical Garden, St. Louis

MEXU - Herbario Nacional, Universidad Nacional Autonoma de Mexico

NY - New York Botanical Garden, Bronx

P - Museum Nationale d' Historie Naturelle, Paris, France

SI - Instituto de Botanica Darwinion, Buenos Aires, Argentina

TEX - University of Texas, Austin

US - United States National Herbarium, Smithsonian Institution, Washington, D.C.

VEN - Instituto Botanico, Caracas, Venezuela

W - Naturhistorisches Museum, Botanische Abteilung, Wien, Austria

WIS - University of Wisconsin, Madison

XAL - Instituto Nacional de Investigaciones sobre Recursos Bioticos, Veracruz, Mexico.

B. Field Studies

Field work was conducted during the last six months of 1985 in many localities of Mexico. Plant collections were not carried out in other countries due to the lack of economic support. By means of herbarium loans from different countries of the world the remainder material that was not collected on this field trip was obtained. Collection sites were determined by information from herbarium labels, correspondence with professional systematists in the areas of interest, and information available in the literature. Standard collection procedures were followed. Complete specimens were pressed, and then

dried at the National Herbarium of Mexico (MEXU). All specimens were collected in multiple sets for further distribution to various herbaria. Leaves, culms, and inflorescences were preserved in Formalin-Acetic-Alcohol (FAA) for anatomical and morphological studies. Flowering material was fixed in Newcomer's solution (Newcomer, 1953) for chromosome counts.

C. Morphological Studies

About 2500 specimens were obtained from the different herbaria. For most taxa, enough specimens were procured, but, for some species, especially the African ones, the number of specimens was small or sometimes the material was incomplete (lack of inflorescences, rhizomes or subterranean parts, or leaves). Many type specimens of Sorghastrum species were obtained. Sometimes the complete plant was available, but frequently just fragments of the type specimens (some spikelets) were procured.

Standard measurements were recorded. Length and width data were collected for leaves, sheaths, spikelets, glumes, as well as for sterile and fertile lemmas, in each specimen examined. Length measurements were obtained for plant height, ligules, peduncle, inflorescence, and sterile pedicel. Leaf length was measured from the tip of the blade to the ligule, and width was measured at the widest point. Sheath length was taken from the ligule to the node of insertion, and width was measured at the middle point. Spikelet dissections were done in Pohl's solution (Pohl, 1965). The length of the spikelet was measured from the base of

Glume I to the tip of the longest bract. The length of the glumes and lemmas was measured from their base to the tip. A proportion between the length of each awn and the spikelet length was obtained. The width was always measured at the widest point. The inflorescence length was measured from the tip to the insertion of the basal branch. The peduncle was measured from the basal branch insertion to the last culm node.

According to the number of herbarium specimens available for each species, a decision was made for measuring a complete set of specimens or a representative subset. I have followed the agrostological terminology and the technical names used by Pohl (1980).

Some qualitative data was also observed, such as inflorescence shape, color of spikelets and nodes and pubescence of leaves, culm, sheath, glumes, and sterile pedicel.

D. Chromosome Studies

Young and unexpanded inflorescences of individuals of Sorghastrum were fixed in Newcomer's solution to obtain meiotic material for chromosome studies. Anthers were dissected out, squashed, and stained with propiocarmine (Sharma and Sharma, 1965).

E. Anatomical Studies

1. Light microscopy

Leaf blade cross sections were made and examined with light microscopy. Samples of leaves were fixed in the field in FAA or taken

from herbarium specimens and softened in Pohl's solution for a week or more before fixation in FAA. After fixation, the leaf material was washed in tap water for 30 minutes, desilicified in 10% aqueous hydrofluoric acid solution for nine days, then rinsed in running water. Dehydration occurred in steps of 25%, 50%, 70%, 95% (two changes) and 100% (two changes) ethanol.

The material was bulk stained in a solution of 1% safranin in 1:1 ethanol:xylene for an hour, then passed through two changes of xylene. Infiltration was made by adding melted paraffin wax (Fisher Tissueprep, 56.5 °C) to the leaf material in xylene followed by two days in an oven at 60 °C to permit complete evaporation of the xylene and slow infiltration of the wax. Cooling at room temperature completed embedment. Sections were cut on a microtome at 7 - 11 μm.

2. Scanning electron microscopy

The scanning electron microscope was used to examine leaf epidermis of Sorghastrum species. Square pieces were cut from mid-portions of leaves, including the midrib. Some leaf samples were mounted without any other treatment, in order to observe the epicuticular wax pattern. Other samples were sonicated in xylene for 12-15 minutes to remove the cuticular covering in order to observe silica bodies, cork cells, and stomata. Specimens were mounted on brass discs with silver paste or double-stick tape and coated with Au-Pd in a Polaron E5100 sputter-coater and viewed at 15 kV in a JEOL JSM-35 scanning electron microscope. Photographs were taken using Polaroid type 665 positive-negative film.

III. CHROMOSOME NUMBERS

Chromosomal and genetic investigations of the grasses have been initiated primarily for two reasons. First, to provide fundamental information for improvement of species by breeding. Second, to supplement morphological data in studies of taxonomy and phylogeny of the Gramineae (Myers, 1947). The latter is the main purpose of the chromosome number determination carried out in this dissertation.

Two different cytological approaches were considered in this work. First, the basic chromosome number of the Andropogoneae was compared with the basic number of Sorghastrum. Second, chromosme numbers of Sorghastrum species were compared in order to aid in explaining the phylogeny and biogeography within Sorghastrum.

Taking in consideration the diverse chromosome counts reported for Andropogoneae, the basic number of x=5 seems generally accepted (Garber 1950, Celarier 1956). Most of the species of Andropogoneae that have been studied have somatic numbers that are multiples of five (Celarier 1959). However, some important disagreements with this generalization have been reported. Clayton and Renvoize (1986) indicated an occasional basic number of x=9, especially occurring in the Rottboelliinae. Furthermore, Celarier and Paliwal (1957) reported a species of Andropogoneae with a meiotic number of n=4, and Sharma and Bhattacharjee (1957) suggested the same basic number for Sorghum. Finally, Celarier (1959) pointed out that Cleistachne sorghoides shows a somatic number of 2n=36. He suggested two different possible amphidiploid origins. First,

the amphidiploid species has been derived from crossing two species with a meiotic number of n=9, which probably was derived from 2n=20 with the loss of one pair of chromosomes followed by chromosome doubling. Second, the amphidiploid species has been derived by crosses between species with two different base numbers, one with n=5 and the other n=4. Celarier supports the latter explanation on the basis of similar reports of Celarier and Paliwal (1957) and Sharma and Bhattacharjee (1957).

Despite of these disagreements, the commonest basic number still considered for the Andropogoneae is x=5.

In Sorghastrum, chromosome counts for 12 species have been reported before. Two new chromosome counts for the species S. nudipes (Davila et al. 142 and 143) and S. brunneum (Davila et al. 196a) are also included in this dissertation. There are no chromosome counts, as far as I know, for Sorghastrum balansae, Sorghastrum chaseae and Sorghastrum contractum (Table 1).

The dominant somatic number among Sorghastrum species is 2n=20 (about 70% of the total number of species); however, other numbers such as 2n=40,60, or even 80 are not rare in certain species. It appears that the basic chromosome number for Sorghastrum is x=10.

There are 10 species of Sorghastrum that only show a somatic number of 2n=20. Five are from South America: S. scaberrimum (Pereira 1982), S. stipoides (Saura 1944; Carnahan and Hill 1961; Pereira 1982 and 1986), S. pellitum (Saura 1944; Pereira 1982), S. minarum (Pereira 1982 and 1986), and S. viride (Pereira 1982). Three of them are from North America: S. secundum (Myers 1947; Garber 1950), S. elliottii (Brown 1950, Garber

1950), and S. nudipes (Davila, Department of Botany, ISU). The species S. brunneum (Davila, Department of Botany, ISU) occurs in Mexico and Central America, and finally S. setosum (Saura 1944; Carnahan and Hill 1961; Davidse and Pohl 1972a; Davidse and Pohl 1974, Pereira 1986) is distributed from Mexico to South America including the Caribbean.

On the other hand, four species have been reported to have higher chromosome numbers than 2n=20. First, Sorghastrum nutans, a widespread species of North America, distributed from Canada to Central Mexico, has been reported to have a somatic number of 2n=20 (Carnahan and Hill 1961), 2n=40 (Church 1929; Brown 1950; Bowden 1960), or even 2n=80 (Gould 1968). Second, Sorghastrum incompletum var. incompletum, an annual variety occurring in Mexico, Central America, and Northern South America, has been reported to have a somatic number of 2n=20 (Pohl and Davidse, 1971) as well as 2n=40 (Davidse and Pohl 1974). Sorghastrum incompletum var. bipennatum is an African variety that is only reported to show a somatic number of 2n=20 (Olorde, 1975). Third, Sorghastrum trichopus of Southern and Southeastern Africa has been twice reported as having a somatic number of 2n=40 (Moffett and Hurcombe 1949; Carnahan and Hill 1961). Finally, Sorghastrum rigidifolium of Central and Southern Africa has a somatic number of 2n=40 (Tateoka 1965) as well as 2n=60 (Garber 1950, Carnahan and Hill 1961).

Table 1. Chromosome numbers in Sorghastrum species

NAME	CHROMOSOME NUMBER 2n	REFERENCES
S. balansae	?	
S. brunneum	20	(Davila, unpublished)
S. chaseae	?	
S. contractum	?	
S. elliottii	20	(Brown, 1950; Garber, 1950)
S. incompletum var. incompletum	20,40	(Pohl and Davidse,1971; Davidse and Pohl, 1974)
S. incompletum var. bipennatum	20	(Olorde, 1975)
S. minarum	20	(Pereira 1982 and 1986)
S. nudipes	20	(Davila, unpublished)
S. nutans	20, 40, 80	(Church, 1929; Brown, 1950; Bowden, 1960; Carnahan and hill, 1961; Gould 1968)
S. pellitum	20	(Saura, 1944; Pereira, 1982)
S. rigidifolium	40,60	(Garber, 1950; Carnahan and Hill, 1961; Tateoka, 1965)
S. scaberrimum	20	(Pereira, 1982)
S. secundum	20	(Myers, 1947; Garber, 1950)
S. setosum	20	(Saura, 1944; Carnahan and Hill, 1961; Davidse and Pohl, 1972a; Davidse and Pohl, 1974; Pereira, 1986)
S. stipoides	20	(Saura, 1944; Carnahan and Hill, 1961, Pereira 1982 and 1986)
S. trichopus	40	(Moffett and Hurcombe, 1949; Carnahan and Hill, 1961)
S. viride	20	(Pereira, 1982)

These results show that the two African species have higher chromosome numbers than most of the species occurring in the New World. One of these African species (Sorghastrum trichopus) is, like S. setosum from the New World, well adapted to swampy or boggy places. It shows

reduction in the awn (straight, usually non-geniculate and sometimes reduced to a mucro). It seems that S. trichopus, as well as S. setosum in the New World, represent an advanced evolutionary line in Sorghastrum. However, S. trichopus is a tetraploid, whereas S. setosum is diploid, representing the common chromosome level in Sorghastrum. In addition, another African species, Sorghastrum rigidifolium, is tetraploid or hexaploid and is well distributed in Central and South Africa. Finally, S. incompletum var. bipennatum is the only taxon in Africa that is reported to have a diploid condition. However S. incompletum var. incompletum from the Americas is known to be diploid (n=20), as well as tetraploid (2n=40).

This latter case represents, in my opinion, an introduction of either one of the varieties. The first choice may be that S. incompletum originated in Africa and was introduced to the Americas, where it developed two different ploidy numbers (2n=20 and 40). The second choice may be to assume that S. incompletum originated in the Americas and was later introduced to Africa, where only a diploid has been reported (2n=20). In my opinion, I find the second choice more plausible, because by this means it is easy to explain the presence of a diploid variety in an African region, where the common numbers are 2n= 40 and 60.

Comparing the basic number of Sorghastrum, x=10 and the commonest somatic number 2n=20 to some selected and related genera of Andropogoneae (Sorghum, Bothriochloa, Andropogon, Dichanthium, Hyparrhenia, and Cleistachne), the following points are observed. With exception of

Cleistachne, the somatic number of these genera support the hypothesis of the Andropogoneae having a basic number of x=5. In addition, along with Sorghastrum, all these genera show euploids having somatic numbers of 2n=20,40,60,80, etc. Even though it is known that about 64% of the grass species are thought to be entirely polyploid (Davidse and Pohl, 1974), it appears that the more widespread genera, such as Bothriochloa and Andropogon show more and higher diversity in chromosome numbers .

Bothriochloa has been reported to have a somatic number of 2n=40 (De Wet 1958; Celarier and Harlan 1958; Carnahan and Hill 1961; Mehra et al. 1962; Tateoka 1965), or even somatic numbers of 2n=120 (Carnahan and Hill 1961).

Andropogon has been commonly reported to show diverse somatic numbers, including commonly 2n=20, 40, 60 (Church 1940; Moffett and Hurcombe 1949; Mehra et al. 1962; Tateoka 1965; Pohl and Davidse 1971; Norrmann 1985). In addition, much higher counts have been reported. Davidse and Pohl (1972b) reported a somatic number of 2n=80; Church (1940) cited a species showing a somatic number of 2n=100, whereas Carnahan and Hill (1961) reported a species having 2n=120 and 180.

The related genera that have a more restricted distribution range usually show less diversity of polyploid numbers. This is the case with Sorghum occurring naturally in Africa, which is reported to have 2n=10, 20, and 40 (Church 1929; Moffett and Hurcombe 1949; Gould 1956; Carnahan and Hill 1961). Dichanthium occurring in Africa and the Mediterranean regions, is cited as showing somatic numbers of 2n=20, 40, and 60 (Gould 1956; Carnahan and Hill 1961; Mehara et al. 1962). Finally, Hyparrhenia,

mainly distributed in Africa, some Asiatic regions and Australia, has been reported to have somatic numbers of 2n=20, 40, 60 (Moffett and Hurcombe 1949; Gould 1956; Carnahan and Hill 1961).

IV. REPRODUCTIVE BIOLOGY

Grasses are mainly wind pollinated, even though some investigators, such as Bogdan (1962), have reported observations of insects feeding on grass pollen. According to my observations, with respect to the genus Sorghastrum and in general for the Andropogoneae, wind pollination seems the common pattern.

With respect to the breeding mechanisms, the grasses have developed two main breeding behaviors. Cross pollination represents a complex incompatibility system, insuring outbreeding; self-pollination promotes self-fertility (Connor 1980). Pereira (1982) carried out breeding experiments on some of the Sorghastrum species inhabiting the Brazilian state of Rio Grande Do Sul, i.e., S. minarum, S. scaberrimum, S. stipoides, S. pellitum, S. viride, and S. contractum (sensu Davila). The reports from this investigation claim that all these species are normally cross-pollinated. Systematic studies have not included the reproductive biology of all species of Sorghastrum.

Finally, and even though there is no information available as to hybridization processes in Sorghastrum, there is indirect evidence suggesting the presence of this biological phenomenon. Sorghastrum pellitum and Sorghastrum viride are South American species that are partially sympatric. The latter tends to inhabit high and mesic zones, whereas S. pellitum is well adapted to live in low and very dry regions (Pampa region, in Argentina). However, my observations based on herbarium specimens indicate that in the overlapping area, different

variants are present. Sometimes some of these are morphologically closer to S. pellitum, but some other specimens are more similar to S. viride. It is possible to observe a whole gradient of intermediate "forms" between S. pellitum and S. viride. Unfortunately, these observations do not demonstrate by themselves that hybridization is taking place.

V. PHENOLOGY

Hartley (1958) pointed out that the Panicoideae (including the tribes Paniceae and Andropogoneae) sensu Hackel, originated in the warmer regions of the Eastern Hemisphere. However, these tribes show different distribution ranges that are related to differences in climatic adaptations. Even though both reach their highest development in hot, moist climates, the Paniceae are characteristic of regions with a long wet season (equatorial belt). On the other hand, the Andropogoneae reach the highest development in monsoonal climates with a short season of heavy rainfall. Consequently, a large proportion of Paniceae occur in areas with a long growing season (late spring to early autumn). On the other hand, the Andropogoneae reach their greatest diversity in regions with a short growing season and high mid-summer rainfall. Phenologically, the expression of the climatic adaptations of these two tribes result in differences in their flowering periods. The Paniceae flower during spring or summer, whereas the Andropogoneae flower mainly in the autumn.

With respect to the genus Sorghastrum, Weaver and Fitzpatrick (1932) followed some of the reproductive steps of Sorghastrum nutans. They found that this species begins its growth late in spring and flowers late in autumn. In addition, based on the information that I obtained from observations of herbarium specimens and from personal field observations indicates that, except for S. pellitum and S. viride, the rest of Sorghastrum species flower mainly during the autumm. The latter species

commonly flower during the spring.

The phenology of the Andropogoneae and of Sorghastrum is undoubtedly important from the taxonomic point of view. However, as is indicated by Matches et al. (1982), this information should be also valuable in agronomic areas. That is, probably some species of Sorghastrum, as well as other Andropogoneae already recognized as good forage grasses, can be used as sources of feed at the time when cool-season forage grasses are less productive.

VI. ECOLOGY

Within the Gramineae, the Andropogoneae is a tropical tribe, particularly inhabiting the savanna zone, extending into warm temperate regions. Specifically, the savanna type vegetation is characterized by having strong and contrasting seasons of high rainfall and drought. Some biotic factors like fire, grazing, and farming have opened establishment possibilities for many grasses in these areas (Clayton and Renvoize, 1986).

The following statements are based upon personal field observations and data obtained from herbarium specimens. In particular, the species of Sorghastrum may inhabit any of three different habitats. First, there is a group of species mainly living in savanna-like vegetation, which occur generally in lowlands with long periods of drought. These regions are mainly inhabited by S. chaseae, S. contractum, S. minarum, S. pellitum, S. viride, and S. incompletum. Except for the last one, the rest are strictly South American species.

Another group of species inhabit pine-oak forests or woodlands, medium elevation grasslands, scrub-like vegetation, and deciduous forests. Usually these regions exist at altitudes of 1000-2500 m. The type of soil may be argillaceous, sometimes sandy, and usually very rocky. The species living in this kind of habitat are S. brunneum, S. elliottii, S. nudipes, S. scaberrimum, S. secundum and S. rigidifolium. The last one represents an African species adapted mainly to sandy woodlands, but sometimes to swampy places. S. brunneum, S. elliottii, S.

nudipes, and S. secundum are a North American group, that along with S. scaberrimum from South America, mainly occur in temperate regions. This means that S. scaberrimum represents the only South American element adapted to temperate forest-type vegetation.

A third group of species inhabit swampy or boggy places. These environmental requirements are shared by S. setosum from the Americas and S. trichopus from Africa. It is pointed out, on some herbarium labels, that these two species are well adapted to drastic changes of alternating floodings and dry conditions.

The last two species, S. nutans in North America and S. stipoides in South America, represent two widespread species inhabiting various kinds of habitats. S. nutans occurs in dry scrub-like vegetation or in the Northern temperate prairies of the United States.

VII. LEAF ANATOMY

A. Leaf Cross Section

1. Introduction

A survey of the leaf anatomy of all species of Sorghastrum was carried out. Leaf anatomy studies, including leaf cross sections, have been shown to be an important tool for agrostologists (Gould, 1968). However, no previous anatomical survey of the genus exists. It is not listed by Metcalfe (1960) in his work, Anatomy of the Monocotyledons, in the part dealing with the Gramineae or any other anatomical revision.

Many anatomical sections from specimens of different herbaria of the world, as well as material from my own collections, were made. In addition, repeated anatomical sections from different individuals of each species were prepared, in order to sample the variability within each taxon. The terminology and figures used in this section are based on Ellis (1976).

2. General considerations

The leaf cross section survey of Sorghastrum species show various important characters. From the results obtained, the following considerations should be pointed out:

I. The outline of the lamina in Sorghastrum may be open or inrolled. The former condition is shown by S. contractum, S. elliottii, S. nudipes, S. nutans, S. scaberrimum, S. secundum, S. stipoides, and S. viride. The rest of the species show inrolling of both margins, or sometimes only one of them. In general terms, the species showing inrolled leaves inhabit

dry places, especially savanna-type vegetation. On the other hand, those species having flat leaves are mainly distributed in woodlands. However, many exceptions are observed.

II. The midrib in Sorghastrum is mainly compound (formed by more than one vascular bundle), however, S. minarum and S. rigidifolium show a simple midrib (formed by only one first order vascular bundle), without association of parenchyma cells. These parenchyma cells probably originated later in the rest of the species.

III. Even though the number of vascular bundles is not constant within all the species of Sorghastrum, all of them show about 4-9 first order vascular bundles on either side of the midrib.

IV. The vascular bundles in Sorghastrum are of three types, i.e., first, second and third order vascular bundles. The shape of these bundles, as seen in transectional view, is regularly rounded or vertically elongated; however, the angular form also occurs, especially for the third order bundles.

V. As a C_4 plant, with NADP-MS as the specific photosynthetic pathway (Hattersley and Watson 1976), this genus shows a single vascular bundle sheath. These sheaths completely surround the second and third order vascular bundles. On the other hand, the sheath incompletely surrounds the first order vascular bundles due to an interruption of abaxial sclerenchyma.

VI. The first order vascular bundle sheaths usually have 15-20 parenchyma cells. S. trichopus and S. setosum, however, generally show

10-15 parenchyma cells. Probably this difference in numbers is correlated to the aquatic adaptation of these two latter species. The second order vascular bundle sheaths of Sorghastrum species generally consist of 7-12 parenchyma cells. The third order vascular bundle sheaths are usually formed by 4-9 parenchyma cells.

VII. The parenchyma cells forming these sheaths may have their radial walls straight and the tangential ones inflated (sometimes the outer tangential wall is also straight). However, occasionally the parenchyma cells might show a rounded or even an irregular shape.

VIII. The bulliform cells are always present in the adaxial surface of the leaf. Bulliform groups are generally fan-shaped, but occasionally they form restricted groups of large, parallel-sided cells (inner tangential wall same length, or slightly shorter than the outer tangential wall). The latter is shown by S. chaseae, S. scaberrimum, S. pellitum, S. viride, S. contractum, and S. elliottii.

3. Descriptions

Sorghastrum Nash

OUTLINE OF THE LAMINA: open, expanded or inrolled. RIBS AND FURROWS: present on the adaxial surface or in both surfaces, or absent, ribs generally rounded and present over first and second order vascular bundles. MIDRIB: simple (with one first order vascular bundle without parenchyma cells associated) or compound (with several vascular bundles forming the midrib and parenchyma cells associated) (Fig. 3B); adaxial sclerenchyma is present, forming subepidermal layers or hypodermal bands

in the adaxial surface, and forming girders of different sizes and shapes (Figs. 3G and 3H). VASCULAR BUNDLE ARRANGEMENT: variable, the arrangement near the margin differs from the remainder, all vascular bundles situated closer to the abaxial surface, about 4-9 first order vascular bundles in either side of the midrib. VASCULAR BUNDLES: First Order Bundles rounded, vertically elongated or ovoid; the phloem completely surrounded by thick-walled fibres; metaxylem vessels wide, their walls thickened; Second Order Bundles rounded or angular; Third Order Bundles rounded or angular, the xylem and phloem groups distinguishable or consisting of only a few vacular strands. VASCULAR BUNDLE SHEATHS: a single bundle sheath, rounded, or vertically elongated; complete or incompletely surrounding the bundles; parenchyma sheath cells of diverse shapes and sizes, distinct from chlorenchyma cells, with their walls distinctly thickened and presenting large and specialized chloroplasts; the chloroplasts situated either the center or in entire cell lumen (Figs. 5N and 5O). SCLERENCHYMA ASSOCIATED WITH VASCULAR BUNDLES: in first and second order vascular bundles, the fibers forming girders at both surfaces (Fig. 6J); in third order bundles the girders present in the abaxial surface; the fibers may contact or interrupt the bundle sheath. SCLERENCHYMA IN LEAF MARGIN: fibers forming a hood (sclerenchyma extensions situated below the ultimate and penultimate lateral bundle) (Fig. 6I). MESOPHYLL: Chlorenchyma radiate (Fig. 7A), forming a single layer of tabular cells that may be interrupted above and below the bundles by sclerenchyma or colorless parenchyma girders (Fig. 7B); Colorless Cells thin-walled parenchyma

cells of irregular size and shape, closely associated with inflated bulliform cells, smaller and narrower than bulliform cells, forming two extensions, one on either side of the vascular bundle (Fig. 7C). EPIDERMAL CELLS: the outer walls thickened and covered by a distinct, thick cuticle continuous over the epidermal cells (Fig 8D); Bulliform Cells only present at the adaxial surface, generally in fan-shaped groups, seldom forming restricted groups of large, parallel-sided cells (inner tangential wall same length or slightly shorter than the outer tangential wall); Microhairs generally present at one or both surfaces, sunken between the epidermal cells; Papillae lacking or present, the distal outer wall markedely thickened.

1. Sorghastrum balansae (Hackel) Davila

OUTLINE OF THE LAMINA: inrolled from one or both margins (Figs. 1D and 1E). RIBS AND FURROWS: lacking. MIDRIB: compound, formed by 4-9 vascular bundles, the median bundle structurally distinct, showing a raised and flattened adaxial side, parenchyma cells are always associated (Figs. 3C and 3F). VASCULAR BUNDLE ARRANGEMENT: about 7-9 first order vascular bundles on either side of midrib. VASCULAR BUNDLES: First Order Bundles rounded, metaxylem vessels circular (Fig. 4K); Second Order Bundles vertically elongated (Fig. 4J); Third Order Bundles rounded or vertically elongated, xylem and phloem groups distinguishable (Figs. 4A and 4B). VASCULAR BUNDLE SHEATHS: First Order Vascular Bundle Sheaths rounded, incomplete due to an abaxial interruption of a wide abaxial sclerenchyma girder (Figs. 5A and 5D), about 16-18 parenchyma cells

comprise the sheath, sheath cells with the radial walls straight and the tangential walls inflated (Fig. 5F), all cells of similar shape and frequently of similar size, sometimes with a gradation of size, the largest cells adaxially situated (Fig. 5L); Second Order Vascular Bundle Sheaths vertically elongated, completely surrounding the vascular bundle (Figs. 5A and 5C), about 6-10 parenchyma cells comprising the sheath, sheath cells of irregular shape, but same size (Figs. 5I and 5K); Third Order Vascular Bundle Sheaths rounded or slightly elongated, completely surrounding the bundle, about 6 parenchyma cells comprise the sheath, sheath cells or irregular shape, but same size (Figs. 5B and 5I). SCLERENCHYMA ASSOCIATED WITH VASCULAR BUNDLES: First Order Vascular Bundles at the adaxial surface, a small, equidimensional girder contacting the bundle sheath; at the abaxial surface, a small, equidimensional girder interrupting the bundle sheath (Figs. 6C, 6D, 6G, and 6H); Second Order Vascular Bundles on both surfaces, small, equidimensional girders contacting the bundle sheath (Figs. 6C, 6D and 6G); Third Order Vascular Bundles a small, equidimensional girder is only present at the abaxial surface, the sclerenchyma contacts the bundle sheath (Fig. 6G). EPIDERMAL CELLS: Bulliform Cells forming fan-shaped groups, situated at the bases of the furrows (Fig. 8C).

Specimens examined: Chase 11919 (US); Jorgensen 4574 (MO); Macedo 2130 (US); Pedersen 3287 (US).

2. Sorghastrum brunneum Swallen

OUTLINE OF THE LAMINA: loosely inrolled (Fig. 1E). RIBS AND FURROWS: lacking, only slightly undulating, with no regular pattern

associated with the vascular bundles (Fig. 1B). MIDRIB: compound, formed by 6-9 vascular bundles, the median bundle structurally distinct, U-shaped, parenchyma cells in the adaxial surface are always associated to these vascular bundles (Figs. 3C and 3D). VASCULAR BUNDLE ARRANGEMENT: 5-6 first order vascular bundles on either side of the margin. VASCULAR BUNDLES: First Order Bundles ovoid, metaxylem vessels circular (Fig. 4M); Second Order Bundles circular (Fig. 4I); Third Order Bundles circular, the vascular system consisting of a few vascular strands or sometimes xylem and phloem groups distinguishable (Figs. 4G and 4H). VASCULAR BUNDLE SHEATHS: First Order Vascular Bundle Sheaths vertically elongated, incomplete due to an abaxial interruption of broad girders of sclerenchyma (Figs. 5B and 5D), about 16-19 parenchyma cells comprising the sheath, sheath cells with the radial and outer tangential walls straight, the inner tangential wall inflated (Fig. 5G), cells with similar size; Second Order Vascular Bundle Sheaths rounded, completely surrounding the bundle (Figs. 5A and 5C), about 8-10 parenchyma cells comprising the vascular bundle sheath, sheath cells with the radial and outer tangential walls straight, the inner tangential wall inflated, all cells similar in shape and size or sometimes with a gradation in size with the largest cells adaxially situated (Figs. 5G and 5L); Third Order Vascular Bundle Sheaths rounded, completely surrounding the bundle (Figs. 5A and 5C), about 6-7 parenchyma cells comprise the bundle, sheath cells with the radial and outer tangential walls straight, the inner tangential wall inflated, all cells of the same shape and size (Fig. 5G).

SCLERENCHYMA ASSOCIATED WITH VASCULAR BUNDLES: First Order Vascular Bundles at the adaxial surface, a small equidimentisonal girder contacting the bundle sheath; at the abaxial surface, a small, equidimensional girder interrupting the bundle sheath (Figs. 6G and 6H); Second Order Vascular Bundles on both surfaces, small, thin, subepidermal strips of fibers contacting the bundle sheath (Figs. 6A, 6D and 6E); Third Order Vascular Bundles a very small strip of sclerenchyma is only present at the abaxial surface, the sclerenchyma contacting the bundle sheath (Fig. 6E). EPIDERMAL CELLS: Bulliform Cells forming fan-shaped groups situated at the bases of the furrows (Fig. 8C); Papillae thickened (Fig. 8F).

Specimens examined: Johnston 6024 (LL); Molina and Molina 27628 (F); Pohl & Davidse 12139 (ISC); Rzedowski 121159 (ENCB); Steyermark 31325 (ENCB); Ventura 4465 (ENCB).

3. Sorghastrum chaseae Swallen

OUTLINE OF THE LAMINA: inrolled from both margins (Fig. 1E). RIBS AND FURROWS: lacking, only slight irregular undulations are present (Fig. 1B). MIDRIB: compound, formed by 3 vascular bundles, the median bundle structurally distinct, parenchyma cells are always associated (Fig. 3B). VASCULAR BUNDLE ARRANGEMENT: about 9 vascular bundles on either side of the midrib. VASCULAR BUNDLES: First Order Bundles rounded, metaxylem vessels angular (FIg. 4K); Second Order Bundles rounded (Fig. 4I); Third Order Bundles vertically elongated, vascular tissue consists only of a few vascular strands (Figs. 4B and 4H). VASCULAR BUNDLE SHEATHS: First Order Vascular Bundle Sheaths rounded,

incomplete due to an abaxial interruption of broad girders (Figs. 5A and 5D), about 15 parenchyma cells comprise the sheath, sheath cells quite irregular in shape, but same size (Fig. 5J); Second Order Vascular Bundle Sheaths rounded, completely surrounding the bundle (Figs. 5A and 5C), about 8 parenchyma cells comprise the sheath, sheath cells quite irregular, but the same size (Fig. 5I); Third Order Vascular Bundle Sheaths rounded, completely surrounding the bundle sheath (Figs. 5A and 5C), about 6 parenchyma cells comprise the sheath, sheath cells very irregular, but similar in size (Fig. 5I). SCLERENCHYMA ASSOCIATED WITH VASCULAR BUNDLES: First Order Vascular Bundles at the adaxial surface, a small equidimensional girder contacting the bundle sheath (Figs. 6C and 6D); at the abaxial surface, a small equidimensional girder interrupting the bundle sheath (Figs. 6G and 6H); Second Order Vascular Bundles on both surfaces, small thin subepidermal strips of fibers contacting the bundle sheath (Figs. 6A, 6D and 6E); Third Order Vascular Bundles a small thin subepidermal strip of fibers is only present at the abaxial surface, the sclerenchyma contacting the bundle sheath (Fig. 6E). EPIDERMAL CELLS: Bulliform Cells forming restricted groups of inflated cells, projecting above the level of the epidermis (Fig. 8A); Microhairs sunken into the epidermal cells, thick and short (Fig. 8E); Papillae very conspicuous, thick walled (Fig. 8F).

Specimen examined: Chase 11644 (US).

4. Sorghastrum contractum (Hackel) Kuhlm & Kuhn

OUTLINE OF LAMINA: V-shaped, wide, open, the arms of the lamina straight (Fig. 1C). RIBS AND FURROWS: lacking, only slight irregular undulations are present (Fig. 1B). MIDRIB: compound, formed by 5 vascular bundles, with one first order vascular bundle different from the others and the reminder second and third order vascular bundles (Fig. 3C); rounded, parenchyma cells are always associated (Fig. 3E). VASCULAR BUNDLE ARRANGEMENT: about 6-7 first order vascular bundles on either side of the midrib. VASCULAR BUNDLES: First Order Bundles rounded, metaxylem vessels circular (Fig. 4K); Second Order Bundles vertically elongated (Fig. 4J); Third Order Bundles vertically elongated, the vascular tissue consists of only a few vascular strands (Figs. 4B and 4H). VASCULAR BUNDLE SHEATHS: First Order Vascular Bundle Sheaths rounded, incomplete due to an abaxial interruption of sclerenchyma girders (Figs. 5A and 5D), about 14-18 parenchyma cells comprising the sheath, sheath cells with the radial walls straight and the tangential walls inflated, all cells of similar shape and size (Fig. 5F); Second Order Vascular Bundle Sheaths rounded, completely surrounding the bundle (Figs. 5A and 5C), about 9-12 parenchyma cells comprising the sheath, sheath cells with the radial walls straight and the tangential walls inflated, all cells of similar shape and size (Fig. 5F); Third Order Vascular Bundle Sheaths rounded, sheath completely surrounding the bundle (Figs. 5A and 5C), about 6-7 parenchyma cells comprising the sheath, sheath cells with the radial walls straight and the tangential walls inflated, all cells of similar shape and size (Fig. 5F). SCLERENCHYMA

ASSOCIATED WITH VASCULAR BUNDLES: First Order Vascular Bundles at the adaxial surface, a small equidimensional girder contacting the bundle sheath (Figs. 6C and 6D); at the abaxial surface, a small equidimensional girder interrupting the bundle sheath (Figs. 6G and 6H); Second Order Vascular Bundles in both surfaces, a small equidimensional girder contacting the bundle sheath (Figs. 6A, 6D and 6E); Third Order Vascular Bundles a small, thin strip of sclerenchyma contacting the bundle sheath only at the abaxial surface (Fig. 6E). EPIDERMAL CELLS: Bulliform Cells forming restricted groups of inflated cells, projecting above the level of the epidermis (Fig. 8A).

Specimens examined: Chase 8723(US); Chase 10898 (US); Goodland & Maycock 499 (NY);Holway & Holway 1499(US).

5. Sorghastrum elliottii (Mohr) Nash

OUTLINE OF THE LAMINA: expanded flat or rarely V-shaped (Figs. 1A and 1C). RIBS AND FURROWS: lacking, only slightly undulating, with no regular pattern associated with the vascular bundles (Fig. 1B). MIDRIB: compound, formed by 3 vascular bundles, with a raised and flattened adaxial side, parenchyma cells in the adaxial surface are always associated to these vascular bundles (Fig. 3F). VASCULAR BUNDLE ARRANGEMENT: 5-6 first order vascular bundles on either side of the margin. VASCULAR BUNDLES: First Order Bundles vertically elongated, metaxylem vessels circular (Fig. 4L); Second Order Bundles vertically elongated (Fig. 4J); Third Order Bundles angular, the vascular system consisting of a few vascular strands (Fig. 4C). VASCULAR BUNDLE SHEATHS:

First Order Vascular Bundle Sheaths rounded or slightly vertically elongated, incomplete due to an abaxial interruption of broad girders of sclerenchyma (Figs. 5A, 5B and 5D), about 11-12 parenchyma cells comprising the sheath, sheath cells with the radial walls straight and the tangential walls inflated, sometimes the outer tangential wall straight (Figs. 5F and 5G), cells with similar size, or sometimes with various sizes, i.e., a gradation of sizes, with the largest cells in the center of each side (Fig. 5M); Second Order Vascular Bundle Sheaths rounded or vertically elongated, completely surrounding the bundle (Figs. 5A, 5B and 5C), about 8-10 parenchyma cells comprising the vascular bundle sheath, sheath cells with the radial walls straight and the tangential ones inflated, cells of similar or different size (Figs. 5F and 5K); Third Order Vascular Bundle Sheaths rounded or vertically elongated, completely surrounding the bundle (Figs. 5A, 5B and 5C), about 6 parenchyma cells comprise the bundle, sheath cells with the radial and outer tangential walls straight, the inner tangential wall inflated, all cells of the same size (Fig. 5G). SCLERENCHYMA ASSOCIATED WITH VASCULAR BUNDLES: First Order Vascular Bundles at the adaxial surface, a small and thin subepidermal strip of fibres contacting the bundle sheath (Figs. 6A and 6D); at the abaxial surface, a small, equidimensional girder interrupting the bundle sheath (Figs. 6G and 6H); Second Order Vascular Bundles in both surfaces, small, thin, subepidermal strips of fibers contacting the bundle sheath (Figs. 6A, 6D and 6E); Third Order Vascular Bundles a very small strip of sclerenchyma is only present at the abaxial surface, the sclerenchyma contacting the bundle sheath (Fig. 6E).

EPIDERMAL CELLS: Bulliform Cells forming restricted groups of large inflated cells at the same level with the general epidermal surface (Fig. 8B).

Specimens examined: Blomquist 9859 (F); Chapman 4639 (NY); Godfrey 76630 (MO); Kearney 942 (US); King 2205 (TEX); York s.n. (MO).

6. Sorghastrum incompletum (Presl) Nash

OUTLINE OF THE LAMINA: expanded, sometimes gently undulating (Figs. 1A and 1B). RIBS AND FURROWS: lacking. MIDRIB: compound, formed by three vascular bundles, U-shaped, much thicker than the rest of the lamina, parenchyma cells are always associated (Fig. 3D). VASCULAR BUNDLE ARRANGEMENT: 5-8 first order vascular bundles, on either side of the midrib. VASCULAR BUNDLES: First Order Bundles rounded to egg-shaped (broadest side adaxial), metaxylem vessels angular (Figs. 4K and 4M); Second Order Bundles rounded or vertically elongated (Figs. 4I and 4J); Third order Bundles rounded, with xylem and phloem groups distinguishable (Figs. 4A and 4G). VASCULAR BUNDLE SHEATHS: First Order Vascular Bundle Sheaths rounded to vertically elongated, incomplete due to an abaxial interruption of a broad girder (Figs. 5A, 5B and 5D), about 13-16 parenchyma cells comprise the sheath, sheath cells with the radial walls straight and the tangential walls inflated, similar in both shape and size (Fig. 5F); Second Order Vascular Bundle Sheaths rounded to vertically elongated, completely surrounding the bundle (Figs. 5A, 5B and 5C), about 7-9 parenchyma cells comprise the sheath, sheath cells irregular in shape or sometimes with the radial walls and either one of

the tangential walls straight, the reminder tangential wall inflated, all the same size (Figs. 5G, 5H and 5I); Third Order Vascular Bundle Sheaths rounded or vertically elongated, completely surrounding the sheath (Figs. 5A, 5B and 5C), about 5-6 parenchyma cells comprise the bundle sheath, sheath cells irregular, sometimes with the radial and outer tangential walls straight, and the inner tangential wall inflated, all same size (Figs. 5G and 5I). SCLERENCHYMA ASSOCIATED WITH VASCULAR BUNDLES: First Order Vascular Bundles at the adaxial surface, a small, thin subepidermal strip is contacting the bundle sheath (Figs. 6A and 6D); at the abaxial surface, a small equidimensional girder interrupting the bundle sheath (Figs. 6G and 6H); Second Order Vascular Bundles on both surfaces, small, equidimensional girders, or sometimes thin subepidermal strips contacting the bundle sheath (Figs. 6A, 6C, 6D, 6E and 6G); Third Order Vascular Bundles a very small strip, sometimes almost inconspicuous is only present at the abaxial surface, the sclerenchyma contacting the bundle sheath (Fig. 6E). EPIDERMAL CELLS: Bulliform Cells forming fan-shaped groups, situated at the bases of the furrows (Fig. 8C); Papillae wide, the distal outer wall markedly thickened (Fig. 8F).

Specimens examined: Baptista 14175 (US); Breedlove & Raven 13380 (US); Davidse 3138 (VEN); Davila et al. 194, 196, 206, 207 (ISC); Gossweiler s.n. (US); McVaugh 20202 (NY); Ortiz 939 (XAL); Pohl 13743 (ISC); Pohl & Davidse 11396 (ISC), 11550, 11589 (F); Schweinfurth 2486 (US).

7. Sorghastrum minarum (Nees) Hitchcock

OUTLINE OF THE LAMINA: slightly inrolled from one or both margins (Figs. 1D and 1E). RIBS AND FURROWS: lacking, only a few slight undulations are present (Fig. 1B). MIDRIB: simple, a median bundle distinguishable from the reminder first order vascular bundles present, parenchyma cells associated with the vascular bundle absent (Fig. 3A). VASCULAR BUNDLE ARRANGEMENT: 4-8 first order vascular bundles on either side of midrib. VASCULAR BUNDLES: First Order Bundles rounded, metaxylem vessels circular (Fig. 4K); Second Order Bundles rounded or vertically elongated (Figs. 4I and 4J); Third Order Bundles rounded, frequently xylem and phloem groups distinguishable, but sometimes consisting only of a few vascular strands (Figs. 4A, 4G and 4H). VASCULAR BUNDLE SHEATHS: First Order Vascular Bundle Sheaths frequently vertically elongated, sometimes rounded, incomplete due to an abaxial interruption of a wide sclerenchyma girder (Figs. 5A, 5B and 5D), about 13-18 parenchyma cells comprise the sheath, sheath cells with the radial and outer tangential walls straight, the inner tangential walls inflated, all cells similar shape but different size (Figs. 5G and 5K); Second Order Vascular Bundle Sheaths vertically elongated, completely surrounding the vascular bundle (Figs. 5B and 5C), about 10 parenchyma cells comprising the bundle sheath, sheath cells with irregular shape and same size, larger than mesophyll cells (Figs. 5I and 5K); Third Order Vascular Bundle Sheaths rounded or vertically elongated, completely surrounding the vascular bundle (Figs. 5A, 5B and 5C), about 6-7 parenchyma cells comprising the sheath, sheath cells of irregular shape

and similar size (Figs. 5I and 5K). SCLERENCHYMA ASSOCIATED WITH VASCULAR BUNDLES: First Order Vascular Bundles on the adaxial surface, a small, equidimensional girder contacting the sheath (Figs. 6C and 6D); at the abaxial surface, a small, equidimensional girder interrupts the bundle sheath (Figs. 6G and 6H); Second Order Vascular Bundles on both surfaces, small equidimensional girders contacting the bundle sheath (Figs. 6C, 6D and 6G); Third Order Vascular Bundles a small, subepidermal strip is only present at the abaxial surface, the sclerenchyma is contacting the bundle sheath (Fig. 6E). EPIDERMAL CELLS: Bulliform Cells forming fan-shaped groups, situated at the bases of the furrows (Fig. 8C); Papillae with the distal outer wall markedly thickened (Fig. 8F).

Specimens examined: Davidse & Ramamoorthy 10627 (MO); Quarin et al. 2233 (US); Pederson 1033 (US); Schinnini 6537 (CTES);Smith & Klein 12216 (NY).

8. Sorghastrum nudipes Nash

OUTLINE OF THE LAMINA: expanded, flat (Fig. 1A). RIBS AND FURROWS: Absent, only slightly undulating (Fig. 1B). MIDRIB: compound, formed by seven vascular bundles, i.e., one first order vascular bundle and the reminder second and third vascular bundles, rounded, the adaxial side flat, parenchyma cells are always associated (Figs. 3C and 3E). VASCULAR BUNDLE ARRANGEMENT: 5-6 first order vascular bundles in either side of the midrib. VASCULAR BUNDLES: First Order Bundles rounded, metaxylem vessels angular (Fig. 4K); Second Order Bundles rounded (Fig. 4I); Third Order Bundles rounded, xylem and phloem groups distinguishable (Figs. 4A

and 4G). VASCULAR BUNDLE SHEATHS First Order Vascular Bundle Sheaths rounded, incomplete due to an abaxial interruption of broad sclerenchyma girders (Figs. 5A and 5D), about 12 parenchyma cells comprise the sheath, sheath cells with the radial and outer tangential walls straight, the inner tangential wall inflated (Fig. 5G), all cells similar in shape and size, large and inflated, larger than the mesophyll cells (Fig. 5J); Second Order Vascular Bundle Sheaths rounded, completely surrounding the vascular bundle (Figs. 5A and 5C), about 8 parenchyma cells comprise the sheath, cells of irregular shape, but same size (Fig. 5I); Third Order Vascular Bundle Sheaths rounded, completely surrounding the vascular bundle (Figs. 5A and 5C), about 6-7 parenchyma cells comprise the bundle sheath, sheath cells very irregular in shape, but of similar size (Fig. 5I). SCLERENCHYMA ASSOCIATED WITH VASCULAR BUNDLES: First Order Vascular bundles at the adaxial surface, a small, equidimensional girder is contacting the bundle sheath (Figs. 6C and 6D); at the abaxial surface, a small, equidimensional girder is interrupting the bundle sheath (Figs. 6G and 6H); Second Order Vascular Bundles on both surfaces, small equidimensional girders contacting the bundle sheath (Fig. 6A, 6D and 6E); Third Order Vascular Bundles a small, thin, subepidermal strip only present at the abaxial surface, the sclerenchyma contacting the bundle sheath (Fig. 6E). EPIDERMAL CELLS: Bulliform Cells forming fan-shaped groups, situated at the bases of the furrows (Fig. 8C); Papillae wide, outer wall markedly thickened (Fig. 8F).

Specimens examined: Davila et al. 137, 142, 143 (ISC); Gentry et al. 19398 (LL); Palmer 11 (US); Tenorio 10085 (MEXU); Tenorio et al. 9968

(MEXU).

9. Sorghastrum nutans (L.) Nash

OUTLINE OF THE LAMINA: expanded, flat, sometimes slightly inrolled (Figs. 1A and 1D). RIBS AND FURROWS: Adaxial Surface furrows slight, shallow (less than a quarter of the leaf thickness) (Fig. 2A), their base fairly broad (Fig. 2D), with the sides steep, located between first and second order vascular bundles, over third order vascular bundles; ribs rounded, situated over first and second order bundles (Fig. 2E); Abaxial Surface furrows and ribs lacking. MIDRIB: compound, 3-9 vascular bundles, with a median bundle structurally distinct, in addition other third and second order vascular bundles, at the adaxial surface parenchyma cells are always associated (Fig. 3C). VASCULAR BUNDLE ARRANGEMENT: 6-10 first order vascular bundles in either side of midrib. VASCULAR BUNDLES: First Order Bundles rounded or vertically elongated, metaxylem vessels circular (Figs. 4K and 4L); Second Order Bundles vertically elongated (Fig. 4J); Third Order Bundles rounded, xylem and phloem groups distinguishable (Figs. 4A and 4G). VASCULAR BUNDLE SHEATHS: First Order Vascular Bundle Sheaths vertically elongated, incomplete due to an abaxial interruption of a wide sclerenchyma girder (Figs. 5B and 5D), about 19-25 parenchyma cells comprising the sheath, sheath cells with the radial walls straight, and the tangential walls inflated, all same size (Fig. 5F); Second Order Vascular Bundle Sheaths vertically elongated, completely surrounding the bundle (Figs. 5B and 5C), about 9-12 parenchyma cells comprising the bundle, sheath cells of

irregular shape (Fig. 5I), or sometimes with their radial and outer walls straight and the inner wall inflated, all cells same size (Fig. 5G); Third Order Vascular Bundle Sheaths rounded, completely surrounding the bundle (Figs. 5A and 5C), about 8-9 parenchyma cells comprising bundle sheath, sheath cells irregular in shape, but same size (Fig. 5I). SCLERENCHYMA ASSOCIATED WITH VASCULAR BUNDLES: First Order vascular bundles at the adaxial surface, a small, equidimensional girder contacting the sheath (Figs. 6C and 6D); at the abaxial surface, a small, equidimensional girder interrupting the bundle sheath (Figs. 6G and 6H); Second Order Vascular Bundles at both surfaces, small equidimensional girders contacting the bundle sheath (Figs. 6A, 6D and 6E); Third Order Vascular Bundles a thin subepidermal strip, only at the abaxial surface, contacting the bundle sheath (Fig. 6E). EPIDERMAL CELLS: Bulliform Cells forming fan-shaped groups, situated at bases of furrows (Fig. 8C); Microhairs thick and short, sunken in epidermis (Fig. 8E); Papillae wide, outer wall thickened (Fig. 8F).

Specimens examined: Arsene 11562 (US); Davila et al. 89 (ISC); Fernandez s.n. (ENCB); Hinton 9700 (LL); Marsh 986 (TEX); Moldenke 1371 (MO); Moran 5864 (US); Sherff s.n. (F).

10. Sorghastrum pellitum (Hackel) Parodi

OUTLINE OF THE LAMINA: loosely inrolled from one margin, convolute (Fig. 1D). RIBS AND FURROWS: lacking, just a few irregular undulations are present (Fig. 1B). MIDRIB: compound, formed by 5 vascular bundles, i.e., one first order vascular bundle and the reminder second and third order vascular bundles, the median bundle structurally different from the

others (Fig. 3C); rounded, with a raised and flattened adaxial side, parenchyma cells are always associated (Fig. 3F). VASCULAR BUNDLE ARRANGEMENT: about 5-8 first order vascular bundles in either side of the midrib. VASCULAR BUNDLES: First Order Bundles egg-shaped or vertically elongated, metaxylem vessels circular (Figs. 4L and 4M); Second Order Bundles vertically elongated (Fig. 4J); Third Order Bundles rounded, xylem and phloem groups distinguishable (Figs. 4A and 4G). VASCULAR BUNDLE SHEATHS: First Order Vascular Bundle Sheaths vertically elongated, incomplete due to an abaxial interruption of a wide sclerenchyma girder (Figs. 5B and 5D), about 16-17 parenchyma cells comprising the sheath, sheath cells with the radial walls straight and the tangential walls inflated, all cells similar in shape and size (Fig. 5F); Second Order Vascular Bundle Sheaths vertically elongated, completely surrounding the bundle (Figs. 5B and 5C), about 12 parenchyma cells comprise the sheath, sheath cells elliptical, cells of similar shape and size (Fig. 5E); Third Order Vascular Bundle Sheaths rounded, completely surrounding the bundle (Figs. 5A and 5C), about 6-8 parenchyma cells comprising the sheath, sheath cells elliptical and quite irregular in shape and size (Figs. 5I and 5K). SCLERENCHYMA ASSOCIATED WITH VASCULAR BUNDLES: at the adaxial surface, a small, equidimensional girder contacting the bundle sheath (Figs. 6A and 6D); at the abaxial surface, a small, equidimensional girder interrupting the bundle sheath (Figs. 6G and 6H); Second Order Vascular Bundles on both surfaces, small equidimensional girders contacting the bundle sheath (Figs. 6C, 6D and

6G); Third Order Vascular Bundles a small equidimensional girder is only present at the abaxial surface, the sclerenchyma is contacting the bundle sheath (Fig. 6G). EPIDERMAL CELLS: Bulliform Cells forming restricted groups of large, inflated cells, situated at the same level of the general epidermal surface (Fig. 8B); Microhairs sunken between large and inflated epidermal cells, long and thick (Fig. 8E); Papillae thick walled, overarching the stomata (Fig. 8F).

Specimens examined: Archer & Rojas 4869 (US); Cano 4510 (BAB); Clos & Molfino 259 (BAB); Hunziker 4535 (BAB); Montes 15252 (SI); Pedersen 6064 (MO); Schinini & Carnevalli 10411 (CTES); Troncoso 20490 (US)

11. Sorghastrum rigidifolium (Stapf) Chippindall

OUTLINE OF THE LAMINA: loosely inrolled from both margins (Fig. 1E). RIBS AND FURROWS: Adaxial Surface with ribs rounded, situated over first and second order vascular bundles (Fig. 2E); furrows medium size (a quarter to one half the leaf thickness), situated between first and second order vascular bundles, over third order vascular bundles (Fig. 2B); Abaxial Surface presenting only a few irregular undulations. MIDRIB: simple, with only one first order vascular bundle, distinguishable from other first order vascular bundles, parenchyma cells are not associated in the adaxial surface (Fig. 3A). VASCULAR BUNDLE ARRANGEMENT: about 5-6 first order vascular bundles on either side of the midrib. VASCULAR BUNDLES: First order Bundles vertically elongated or egg-shaped, metaxylem vessels angular (Figs. 4L and 4M); Second Order Bundles vertically elongated (Fig. 4J); Third Order Bundles pentagonal, the xylem and phloem groups distinguishable or consisting only of a few

vascular strands (Figs. 4D, 4G and 4H). VASCULAR BUNDLE SHEATHS: First Order Vascular Bundle Sheaths rounded or vertically elongated, incomplete due to an abaxial interruption of broad girders of sclerenchyma (Figs. 5A, 5B and 5D), about 15-18 parenchyma cells comprising the sheath, sheath cells with the radial walls straight and the tangential walls inflated, all similar in size (Fig. 5F); Second Order Vascular Bundle Sheaths rounded or verticaly elongated, completely surrounding the sheath (Figs. 5A, 5B and 5C), about 9-12 parenchyma cells comprising the sheath, sheath cells with the radial walls straight and the tangential walls inflated, all similar in size (Fig. 5F); Third Order Vascular Bundle Sheaths rounded, completely surrounding the sheath (Figs. 5A and 5C), about 7-8 parenchyma cells comprising the sheath, sheath cells with the radial walls straight and the tangential walls inflated, all similar in size (Fig. 5F). SCLERENCHYMA ASSOCIATED WITH VASCULAR BUNDLES: First Order Vascular Bundles at the adaxial surface, a small, equidimensional girder contacting the bundle sheath (Figs. 6C and 6D); at the abaxial surface, a small, equidimensional girder interrupting the bundle sheath (Figs. 6G and 6H); Second Order Vascular Bundles in both surfaces, a small, equidimensional girder contacting the bundle (Figs. 6A, 6D and 6G); Third Order Vascular Bundles a small subepidermal strip of fibers is only present at the abaxial surface, the sclerenchyma contacting the bundle sheath (Fig. 6E). EPIDERMAL CELLS: Bulliform Cells forming fan-shaped groups, situated at the bases of the furrows (Fig. 8C); Microhairs thick and short with sunken bases, especially located in the adaxial

surface (Fig. 8E); Papillae wide, with the outer wall markedly thickened (Fig. 8F).

Specimens examined: Ekman s.n. (LL); Greenway & Rawlines 9376 (US); Richards 17686 (MO); Vesey & Fitzgerald 3218 (MO); Wright 3896 (NY).

12. Sorghastrum scaberrimum (Nees) Herter

OUTLINE OF THE LAMINA: V-shaped (due to a projecting keel), very open (Fig. 1C). RIBS AND FURROWS: lacking, surface only slightly undulating, without any regular pattern (Fig. 1B). MIDRIB: compound, formed by 9 vascular bundles, with one first order vascular bundle different from the others and the reminder second and third order vascular bundles, U-shaped (Figs. 3C and 3D). VASCULAR BUNDLE ARRANGEMENT: 5-7 first order vascular bundles on either side of the margin. VASCULAR BUNDLES: First Order Bundles vertically elongated, metaxylem vessels angular (Fig. 4L); Second Order Bundles rounded (Fig. 4I); Third Order Bundles angular, xylem and phloem groups not distinguishable (Figs. 4E, 4F and 4H). VASCULAR BUNDLE SHEATHS: First Order Vascular Bundle Sheaths vertically elongated or rounded, incomplete due to an abaxial interruption of a broad girder of sclerenchyma (Figs. 5A, 5B and 5D), about 15-20 parenchyma cells comprise the sheath, sheath cells rounded, all cells similar in shape and size (Fig. 5E); Second Order Vascular Bundle Sheaths vertically elongated, the sheath completely surrounding the bundle (Figs. 5B and 5C), about 10-11 parenchyma cells comprise the sheath, sheath cells with the radial walls straight and the tangential walls inflated, cells of similar shape but different size i.e. with the largest cells adaxially situated (Figs. 5F and 5L); Third Order

Vascular Bundle Sheaths rounded, completely surrounding the bundle (Figs. 5A and 5K), about 4-6 parenchyma cells comprising the sheath, sheath cells very irregular, same size (Fig. 5I). SCLERENCHYMA ASSOCIATED WITH VASCULAR BUNDLES: First Order Vascular Bundles on the adaxial surface, a small, equidimensional girder is contacting the bundle sheath (Figs. 6C and 6D); at the abaxial surface, a small, equidimensional girder is interrupting the bundle sheath (Figs. 6G and 6H); Second Order Vascular Bundles on both surfaces, small, equidimensional girders contacting the bundle sheath (Figs. 6C, 6D and 6G); Third Order Vascular Bundles a small, thin subepidermal strip is only present at the abaxial surface, the sclerenchyma contacting the bundle sheath (Fig. 6E). EPIDERMAL CELLS: Bulliform Cells forming restricted groups of large inflated cells, occurring at the same level of the epidermis (Fig. 8B); Microhairs embedded between large, inflated epidermal cells, thick and short (8E). Specimen examined: Chase 9841 (MO); Dombrowski 9595 (ISC); Reitz & Klein 10794 (US); Smith & Klein 16073 (US).

13. Sorghastrum secundum (Ell.) Nash

OUTLINE OF THE LAMINA: V-shaped, the arms very open and almost straight, the two halves of the lamina symmetrical on either side of the midrib (Fig. 1C). RIBS AND FURROWS: Adaxial Surface with ribs rounded and situated over first and second order vascular bundles (Fig. 2E); furrows narrow, their sides almost vertical, the base fairly broad, situated over third order vascular bundles, the depth of the furrows about a quarter to half the leaf thickness (Figs. 2B and 2D); Abaxial

Surface without ribs and furrows. MIDRIB: compound, with a first order vascular bundle, different from the others, in addition to second and third order vascular bundles, rounded, with a raised and flattened adaxial side, parenchyma cells in the adaxial surface are always associated to these vascular bundles (Figs. 3C, 3D and 3F). VASCULAR BUNDLE ARRANGEMENT: about 6 first order vascular bundles on either side of midrib. VASCULAR BUNDLES: First Order Bundles egg-shaped, with the broadest side facing the adaxial surface, metaxylem vessels circular (Fig. 4M); Second Order Bundles rounded (Fig. 4A); Third Order Bundles vertically elongated, the vascular tissue consisting of only a few vascular strands (Figs. 4B and 4H). VASCULAR BUNDLE SHEATHS: First Order Vascular Bundle Sheaths vertically elongated, incomplete due to an interruption of a wide abaxial sclerenchyma girder (Figs. 5B and 5D), more than 15 parenchyma cells comprise the sheath, sheath cells with the radial walls straight and the tangential walls inflated, size very irregular (Figs. 5F and 5K); Second Order Vascular Bundle Sheath vertically elongated, incomplete due to a slight interruption of a narrow, abaxial sclerenchyma girder (Figs. 5B and 5D), about 7 parenchyma cells comprising the sheath, sheath cells with the radial and outer tangential walls straight and the inner tangential wall inflated, their size quite irregular (Figs. 5G and 5K); Third Order Vascular Bundle Sheath vertically elongated, completely surrounding the bundle (Figs. 5B and 5C), about 7 parenchyma cells comprise the bundle sheath, sheath cells with the radial and outer tangential walls straight and the inner tangential wall inflated, all cells same size (Fig. 5G). SCLERENCHYMA

ASSOCIATED WITH VASCULAR BUNDLES: First Order Vascular Bundles at the adaxial surface, a small equidimensional girder contacting the bundle sheath (Figs. 6C and 6D); at the abaxial surface, a small equidimensional girder interrupting the bundle sheath (Figs. 6G and 6H); Second Order Vascular Bundle Sheath at the adaxial surface, a girder deeper than wide contacting the bundle sheath (Figs. 6B and 6D); at the abaxial surface, a small equidimensional girder interrupting the bundle sheath (Figs. 6G and 6H); Third Order Vascular Bundle Sheath a small subepidermal strip of fibers present only at the abaxial surface, the sclerenchyma contacting the bundle sheath (Fig. 6E). EPIDERMAL CELLS: Bulliform Cells forming fan-shaped groups, situated at the bases of the furrows (Fig. 8C); Microhairs thick and short, with sunken bases (Fig. 8E).

Specimens examined: Clos 170 (US); Combs 1193 (US); Correll & Correll 52757 (NY); Curtiss 4019 (NY); Duncan 20663 (F); Nash 753 (NY).

14. Sorghastrum setosum (Griseb.) Hitchcock

OUTLINE OF THE LAMINA: loosely inrolled from both margins, involute (Fig. 1E). RIBS AND FURROWS: Adaxial Surface with ribs rounded, situated over the first and second order vascular bundles (Fig. 2E); furrows narrow, situated between first and second order vascular bundles, i.e., over third order vascular bundles (Fig. 2C); Abaxial Surface with few undulations not regularly associated with the vascular bundles. MIDRIB: compound, with one first order vascular bundle different from the others, in addition to second and third order vascular bundles, parenchyma cells in the adaxial surface are always associated to these vascular bundles

(Fig. 3C). VASCULAR BUNDLE ARRANGEMENT: 5 to 7 first order vascular bundles on either side of midrib. VASCULAR BUNDLES: First Order Bundles egg-shaped, with the broadest side facing the adaxial surface, metaxylem vessels angular (Fig. 4M); Second Order Bundles vertically elongated (Fig. 4J); Third Order Bundles rounded, with xylem and phloem groups distinguishable (Figs. 4A and 4G). VASCULAR BUNDLE SHEATHS: First Order Vascular Bundle Sheaths vertically elongated, incomplete due to an interruption of a wide abaxial sclerenchyma girder (Figs. 5B and 5D), about 15 parenchyma cells comprise the sheath, sheath cells with the radial walls straight and the tangential walls inflated (Fig. 5F), all cells similar in shape, the cells adaxially situated larger than the remainder (Fig. 5L); Second Order Vascular Bundle Sheaths vertically elongated, completely surrounding the bundle (Figs. 5B and 5C), about 12 parenchyma cells comprise the sheath, sheath cells with irregular shape, similar size, large and inflated, larger than mesophyll cells (Figs. 5I and 5J); Third Order Vascular Bundle Sheaths rounded, completely surrounding the bundle sheath (Figs. 5A and 5C), around 10 parenchyma cells comprise the sheath, sheath cells with radial and outer tangential walls straight, inner tangential wall inflated (Fig. 5G), all cells similar in shape and size. SCLERENCHYMA ASSOCIATED WITH VASCULAR BUNDLES: First Order Vascular Bundles at the adaxial surface, a small equidimensional girder contacting the bundle sheath (Figs. 6C and 6D); at the abaxial surface, a small equidimensional girder interrupting the cells of the sheath (Figs. 6G and 6H); Second Order Vascular Bundles at the abaxial and adaxial surfaces small girders contacting the bundle

sheath (Figs. 6A, 6D and 6E); Third Order Vascular Bundles a small subepidermal strip of fibres is only present at the abaxial surface, the sclerenchyma contacting the bundle sheath (Fig. 6E). EPIDERMAL CELLS: Bulliform Cells forming fan-shaped groups, situated at the bases of the furrows (Fig. 8C); Microhairs mainly located at the adaxial surface, thick and short and with sunken bases (Fig. 8E).

Specimens examined: Ahumada et al. 1514 (CTES); Conrad & Conrad 2960 (ISC); Davila et al. 204, 205 (ISC); Davidse & Huber 14949 (MO); Irwind et al. 14553 (NY); Krapovickas et al. 24962 (CTES); Rojas 5592 (US); Steinbach 5428 (US).

15. Sorghastrum stipoides (HBK) Nash

OUTLINE OF THE LAMINA: flat, expanded (Fig. 1A). RIBS AND FURROWS: Adaxial Surface with ribs rounded, situated over the first and second order vascular bundles (Fig. 2E); furrows narrow, in form of a cleft, shallow (less than a quarter of the leaf thickness), situated between first and second order vascular bundles, over third order vascular bundles (Figs. 2A and 2C); Abaxial Surface presenting a few irregular undulations. MIDRIB: compound, formed by 3 vascular bundles, parenchyma cells on the adaxial surface are always associated to these vascular bundles (Fig. 3B). VASCULAR BUNDLE ARRANGEMENT: 5 first order vascular bundles on either side of midrib. VASCULAR BUNDLES: First Order Bundles vertically, metaxylem vessels circular (Fig. 4L); Second Order Bundles vertically elongated (Fig. 4J); Third Order Bundles angular, generaly hexagonal, xylem and phloem groups distinguishable

(Figs. 4E and 4G). VASCULAR BUNDLE SHEATHS: First Order Vascular Bundle Sheaths vertically elongated, incomplete due to an abaxial interruption of broad girders of sclerenchyma (Figs. 5B and 5D), about 18 parenchuyma cells comprising the sheath, sheath cells with the radial walls straight and the tangential walls inflated, all same size (Fig. 5F); Second Order Vascular Bundle Sheaths vertically elongated, incomplete due to an abaxial interruption of broad girders of sclerenchyma (Figs. 5B and 5D), about 11 parenchyma cells comprising the sheath, sheath cells with the radial walls straight and the tangential walls inflated, all same size (Fig. 5F); Third Order Vascular Bundle Sheaths rounded, completely surrounding the bundle (Figs. 5A and 5C), about 8 parenchyma cells comprise the sheath, sheath cells with the radial walls straight and the tangential walls inflated, all same size (Fig. 5F). SCLERENCHYMA ASSOCIATED WITH VASCULAR BUNDLES: First Order Vascular Bundles at the adaxial surface, a small, equidimensional girder contacting the bundle sheath (Figs. 6C and 6D); at the abaxial surface, a small, equidimensional girder interrupting the bundle sheath (Figs. 6G and 6H); Second Order Vascular Bundles at the adaxial surface, a small subepidermal strip of fibers is contacting the bundle sheath (Figs. 6A and 6D); at the abaxial surface, a small, equidimensional girder interrupting the bundle sheath (Figs. 6G and 6H); Third Order Vascular Bundles a small subepidermal strip of fibers is only present at the abaxial surface, the sclerenchyma contacting the bundle sheath (Fig. 6E). EPIDERMAL CELLS: Bulliform Cells forming fan-shaped groups, situated at the bases of the furrows (Fig. 8C); Papillae with the distal outer wall

markedely thickened (Fig. 8F).

Specimens examined: Asplund 6638 (US); Hatschback 15242 (F); Hunziker 1794 (BAB); Mexia 5542 (MO); Reitz & Klein 7732 (US); Schulz 925 (MO).

16. Sorghastrum trichopus (Stapf) Pilger

OUTLINE OF THE LAMINA: flat or loosely inrolled from both margins (Figs. 1A and 1E). RIBS AND FURROWS: Adaxial Surface with ribs rounded, situated over the first and second order vascular bundles (Fig. 2E); furrows narrow, situated between first and second order vascular bundles, over third order vascular bundles (Fig. 2C); Abaxial Surface presenting a few irregular undulations. MIDRIB: compound, formed by three vascular bundles, parenchyma cells in the adaxial surface are always associated to these vascular bundles (Fig. 3C). VASCULAR BUNDLE ARRANGEMENT: 4-5 first order vascular bundles on either side of midrib. VASCULAR BUNDLES: First Order Bundles rounded, metaxylem vessels circular (Fig. 4K); Second Order Bundles vertically elongated (Fig. 4J); Third Order Bundles pentagonal in outline, xylem and phloem groups distinguishable (Figs. 4D and 4G). VASCULAR BUNDLE SHEATHS: First Order Vascular Bundle Sheaths rounded, incomplete due to an abaxial interruption of broad girders of sclerenchyma (Figs. 5A and 5D), about 10-14 parenchyma cells comprising the sheath, sheath cells with irregular shape but similar size, large and inflated, larger than mesophyll cells (Figs. 5I and 5J); Second Order Vascular Bundle Sheaths vertically elongated, incomplete due to an abaxial interruption of broad girders (Figs. 5B and 5D), about 7-9 sheath cells comprise the vascular bundle sheath, sheath cells irregular in

shape but of the same size, large, inflated and longer than mesophyll cells (Figs. 5I and 5J); Third Order Vascular Bundle Sheaths rounded, completely surrounding the bundle (Figs. 5A and 5C), about 5-7 parenchyma cells comprise the sheath, sheath cells irregular in shape but of the same size (Fig. 5I). SCLERENCHYMA ASSOCIATED WITH VASCULAR BUNDLES: First Order Vascular Bundles at the adaxial surface, a small, equidimensional girder contacting the bundle sheath (Figs. 6C and 6D); at the abaxial surface, a small, equidimensional girder interrupting the bundle sheath (Figs. 6G and 6H); Second Order Vascular Bundles at the abaxial and adaxial surfaces with small, equidimensional girders (sometimes the girders deeper than wide) contacting the bundle sheath (Figs. 6B, 6C, 6D, 6F and 6G); Third Order Vascular Bundles a small subepidermal strip of fibers is only present at the abaxial surface, the sclerenchyma contacting the bundle sheath (Fig. 6E). EPIDERMAL CELLS: Bulliform Cells forming fan-shaped groups, situated at the bases of the furrows (Fig. 8C); Microhairs thick and short, with sunken bases, located in both surfaces (Fig. 8E); Papillae with the distal outer wall markedly thickened (Fig. 8F).

Specimens examined: Ellis 2680 (MO); Gonde 32/74 (MO); Robinson 18906 (NY); Smook & Russell 1957 (MO).

17. Sorghastrum viride Swallen

OUTLINE OF THE LAMINA: expanded, flat (Fig. 1A). RIBS AND FURROWS: lacking, only slight undulations are present. MIDRIB: compound, formed by 5 vascular bundles, with one first order vascular bundle different from the others and the remainder second and third order vascular

bundles; rounded, with the adaxial side flat, parenchyma cells are always associated (Figs. 3C and 3E). VASCULAR BUNDLE ARRANGEMENT: about 8-9 first order vascular bundles on either side of the midrib. VASCULAR BUNDLES: First Order Bundles ovoid, broadest side adaxial, metaxylem vessels angular (Fig. 4M); Second Order Bundles rounded (Fig. 4I); Third Order Bundles rounded, xylem and phloem groups distinguishable (Figs. 4A and 4G). VASCULAR BUNDLE SHEATHS: First Order Vascular Bundle Sheaths vertically elongated, incomplete due to an abaxial interruption of sclerenchyma girders (Figs. 5B and 5D), about 16 parenchyma cells comprising the sheath, sheath cells with the radial walls straight and the tangential walls inflated, all cells similar in shape and size (Fig. 5F); Second Order Vascular Bundle Sheaths vertically elongated, completely surrounding the bundle (Figs. 5B and 5C), about 12 parenchyma cells comprising the sheath, sheath cells with the radial walls straight and the tangential walls inflated, all cells similar in size and shape (Fig. 5F); Third Order Vascular Bundle Sheaths rounded, completely surrounding the bundle (Figs. 5A and 5C), about 9 parenchyma cells comprising the sheath, sheath cells with their radial walls straight and the tangential walls inflated (Fig. 5F). SCLERENCHYMA ASSOCIATED WITH VASCULAR BUNDLES: First Order Vascular Bundles on the adaxial surface, a small, equidimensional girder contacting the bundle sheath (Figs. 6C and 6D); at the abaxial surface, a small, equidimensional girder interrupting the bundle sheath (Figs. 6G and 6H); Second Order Vascular Bundles in both surfaces a small, equidimensional girder contacting the bundle

sheath (Figs. 6A, 6D and 6E); Third Order Vascular Bundles a small, thin, subepidermal strip contacting the bundle sheath only at the abaxial surface (Fig. 6E). EPIDERMAL CELLS: Bulliform Cells forming restricted groups of large and inflated cells at the same level with the general epidermal surface (Fig. 8B).

Specimens examined: Burkart & Troncoso 26202 (SI); Hassler 11075 (US); Morong 547 (NY); Quarin 417 (SI); Rosengurtt B-8433 (US). Tressens et al. 415 (CTES).

B. Leaf Epidermis

1. Introduction

Anatomical studies of grasses, including the epidermal surveys, have been shown to be useful tools for the identification and classification of the Gramineae (Prat 1932, 1936; Metcalfe 1960). However, no previous epidermal survey of Sorghastrum exists.

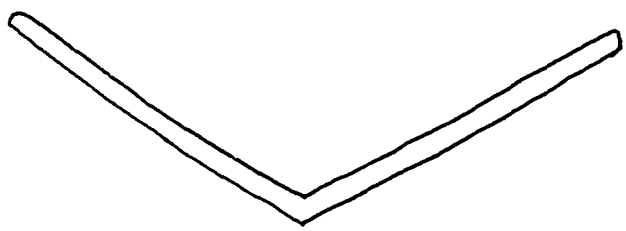
Two different techniques have been mainly used in this study. First, light microscopy that has been long used by all plant anatomists; and second, scanning electron microscopy (SEM), which is a more detailed and useful approach related with modern and fossil epidermal research (Palmer 1976). The latter technique enables examination of certain structures more clearly than with light microscopy. Furthermore, some features have a different aspect when viewed with a scanning electron microscope, as compared to a light microscope (Palmer and Tucker 1981).

The system of classification, terminology, and figures of epidermal features followed is a combination of Palmer and Tucker (1981), Metcalfe

Figure 1. Types of lamina outlines. A. Flat or straight. B. Gently undulating. C. V-shaped. D. Inrolled from one margin. E. Inrolled from both margins

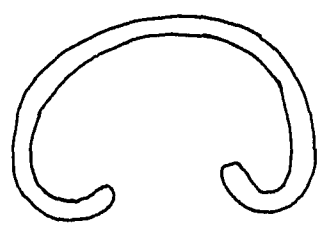
A

B



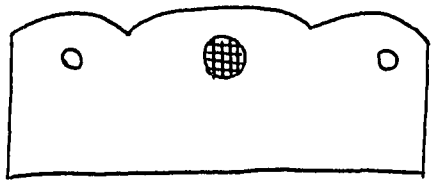
C

D



E

Figure 2. Characteristics of ribs and furrows. A. Furrows slight, shallow (less than a quarter of the leaf thickness). B. Furrows medium (a quarter to one half the leaf thickness). C. Furrows narrow, in form of a cleft. D. Furrows with the base fairly broad. E. Ribs present only over first and second order vascular bundles



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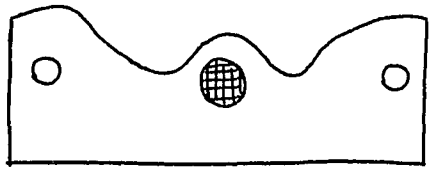

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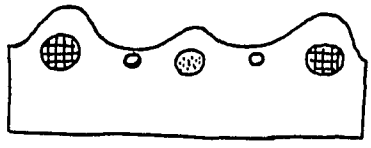

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Figure 3. Characteristics of the midrib. A. Only one vascular bundle present, distinguishable from other first order vascular bundles; no associated parenchyma developed. B. Three vascular bundles present, with parenchyma cells associated. C. A median bundle structurally different and other third and second order bundles forming the midrib. D. Midrib U-shaped, much thicker than the rest of the lamina. E. Midrib rounded, the adaxial side flat. F. Midrib rounded, with a raised and flattened adaxial side. G. The sclerenchyma associated with the midrib is fused forming a hypodermal band. H. Vascular bundles of the midrib showing abaxial girders

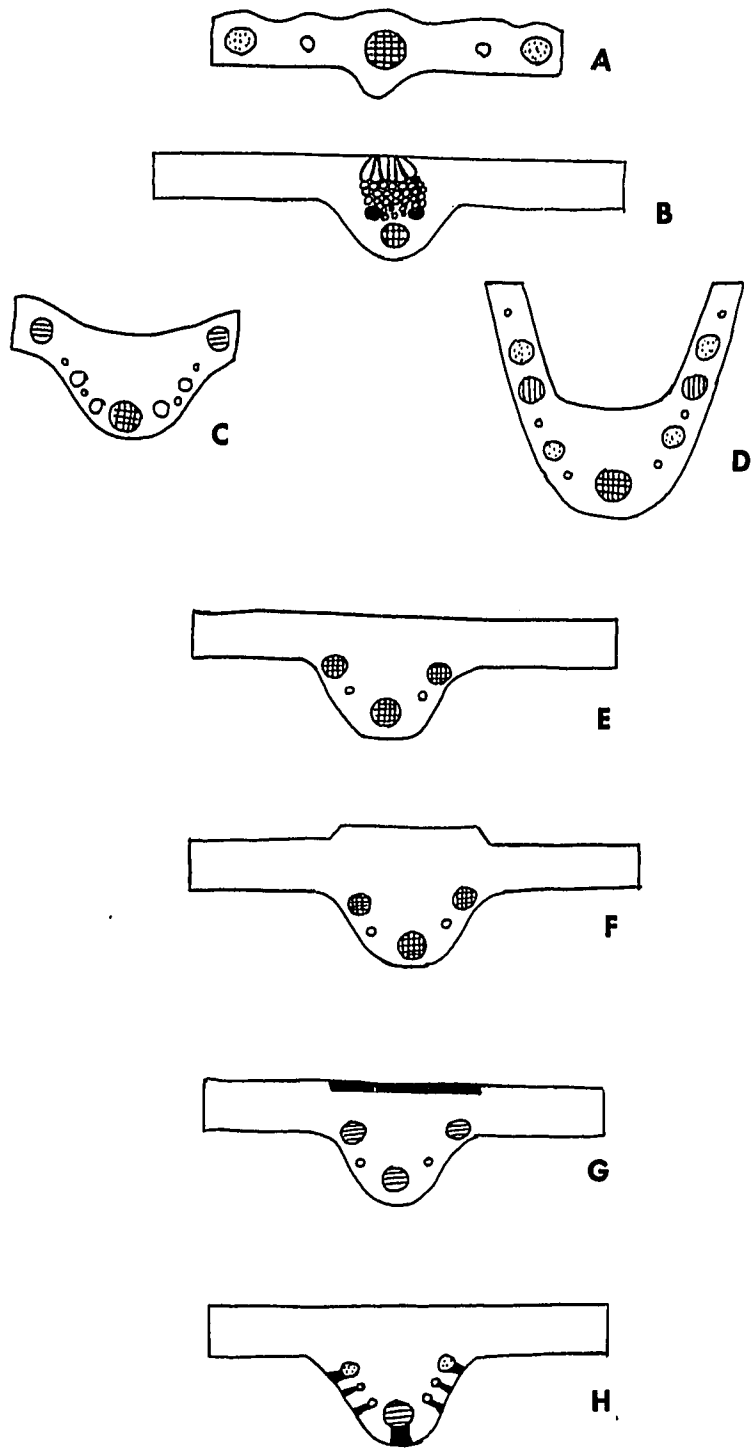
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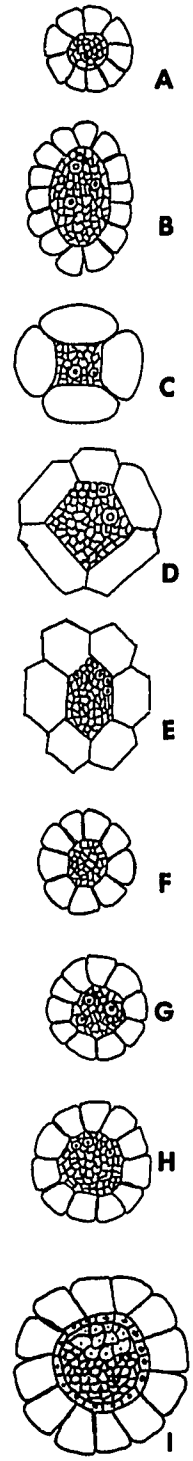
Figure 4. Characteristics of the vascular bundles. A. Third order vascular bundles rounded in outline. B. Third order vascular bundles vertically elongated in outline. C. Third order vascular bundles square-shaped in outline. D. Third order vascular bundles pentagonal in outline. E. Third order vascular bundles hexagonal in outline. F. Third order vascular bundles octagonal in outline. G. Xylem and phloem groups of the third order vascular bundles distinguishable. H. Vascular tissue of the third order vascular bundles, consists of only a few vascular strands. I. Second order vascular bundles rounded in outline. J. Second order vascular bundles vertically elongated in outline. K. First order vascular bundles rounded in outline. L. First order vascular bundles vertically elongated in outline. M. First order vascular bundles ovoid (egg-shaped)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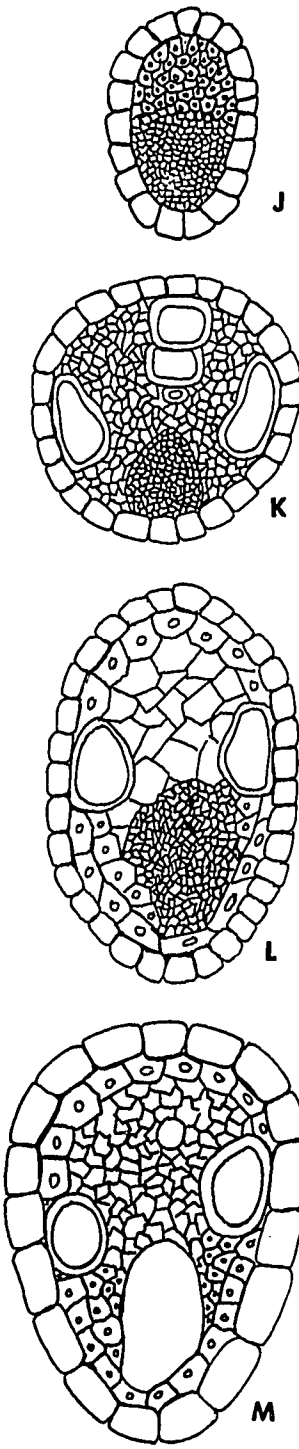
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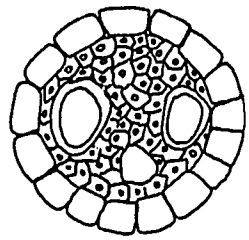
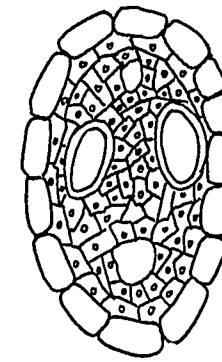
Figure 5. Characteristics of vascular bundle sheaths. A. Sheath rounded. B. Sheath vertically elongated. C. Sheath completely surrounding the bundle. D. Sheath incomplete due to an abaxial interruption of a broad sclerenchyma girder. E. Parenchyma sheath cells rounded or elliptical. F. Sheath cells with the radial walls straight and the tangential walls inflated. G. Sheath cells with the radial and outer tangential walls straight and the inner tangential wall inflated. H. Sheath cells with radial and inner tangential walls straight an the outer tangential wall inflated. I. Sheath cells of irregular shape. J. Sheath cells large and inflated, generally larger than mesophyll cells. K. Sheath cells of different sizes. L. Sheath cells showing a gradation in size, with the largest cells adaxially situated. M. Sheath cells showing a gradation in size, with the largest cells in the center of each side. N. Sheath cells with specialized chloroplasts filling the entire cell lumen. O. Sheath cells with specialized chloroplasts centrally situated



A



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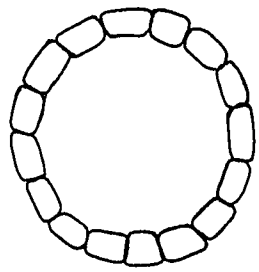

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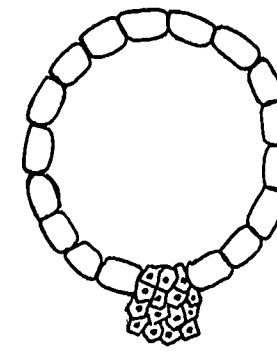

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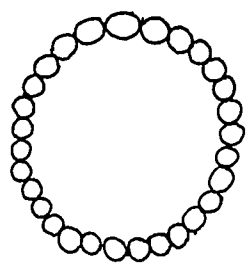

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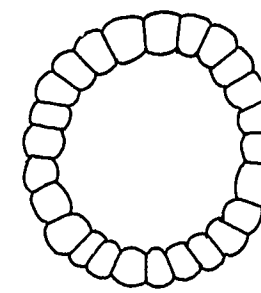

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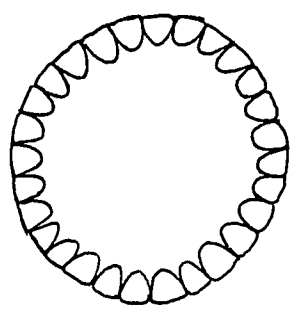

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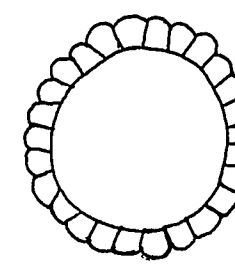

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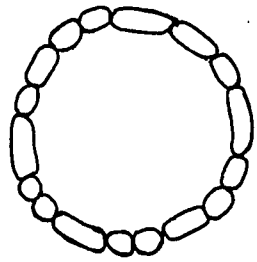

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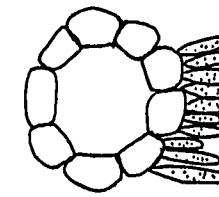

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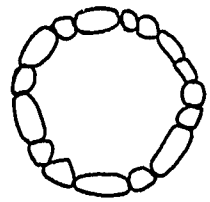

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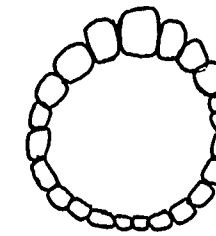

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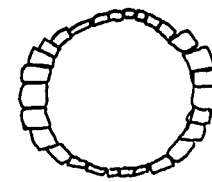

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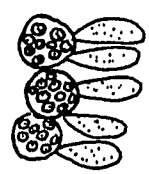

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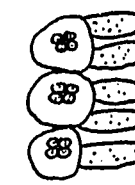

O

Figure 5 (Continued)

Figure 6. Characteristics of the sclerenchyma. A. In the adaxial surface, a very small sclerenchyma girder. B. In the adaxial surface, a narrow girder (deeper than wide). C. In the adaxial surface, an equidimensional girder (as deep as wide). D. Fibres of sclerenchyma in contact with the cells of the bundle sheath. E. In the abaxial surface, a small, thin subepidermal strip. F. In the abaxial surface, a narrow girder (deeper than wide). G. In the abaxial surface, an equidimensional girder (as deep as wide). H. Fibres of sclerenchyma interrupt the bundle sheath. I. A hood of sclerenchyma extending along the abaxial surface of the margin. J. In first and second order vascular bundles, the sclerenchyma fibers forming girders in both surfaces; in the third order vascular bundles, the girders are present only in the abaxial surface

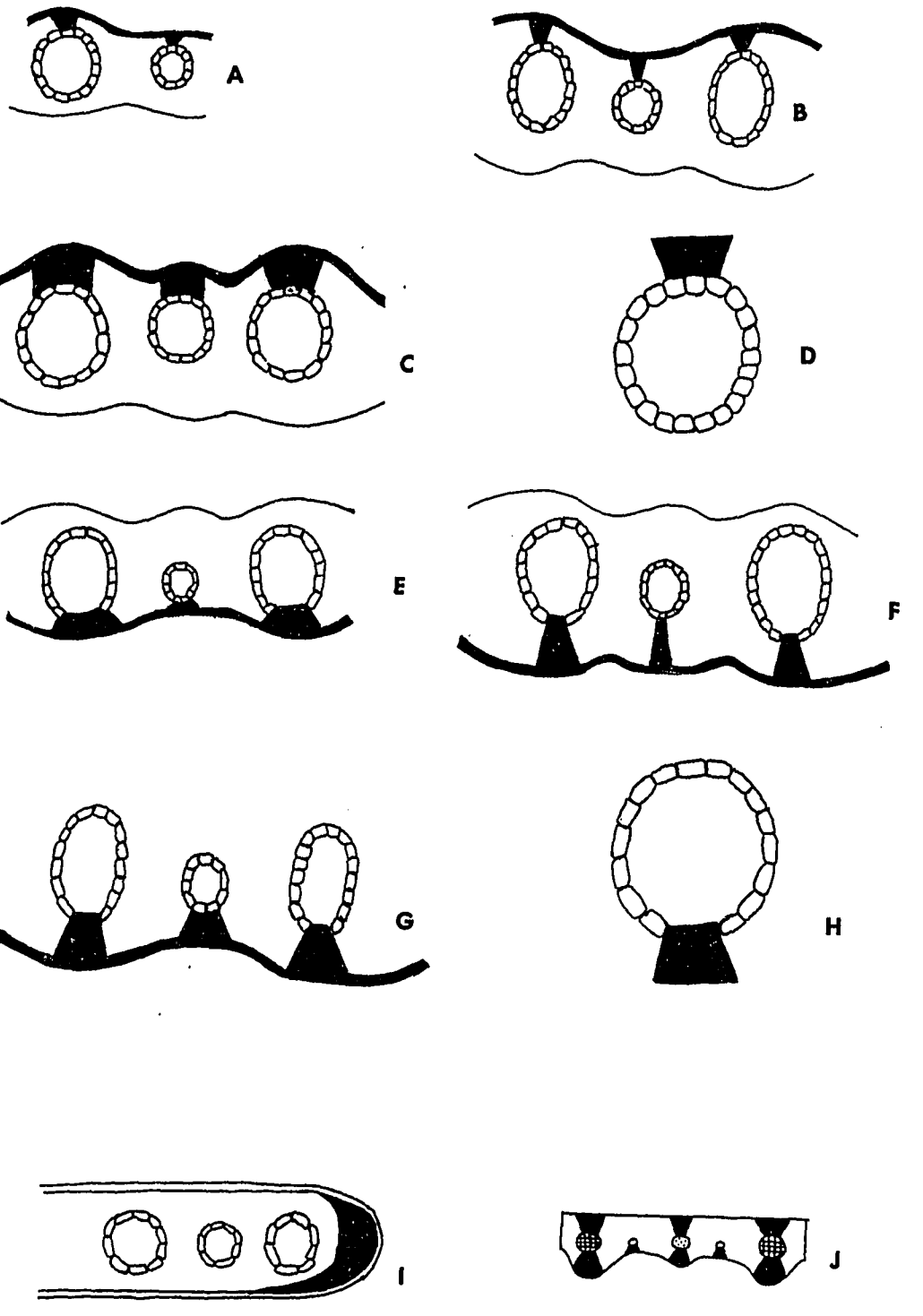
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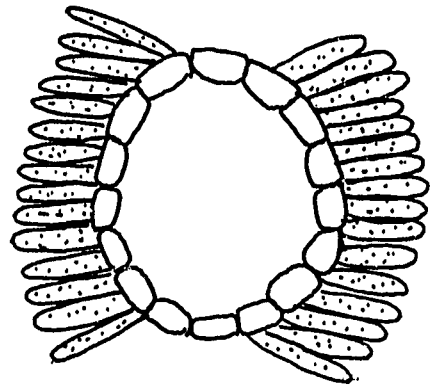
Figure 7. Characteristics of mesophyll cells. A. Chlorenchyma radiate and forming a single layer of tabular cells. B. Radiating chlorenchyma divided by colorless cells. C. Colorless cells with two extensions from each bulliform cell group, one on either side of the vascular bundle



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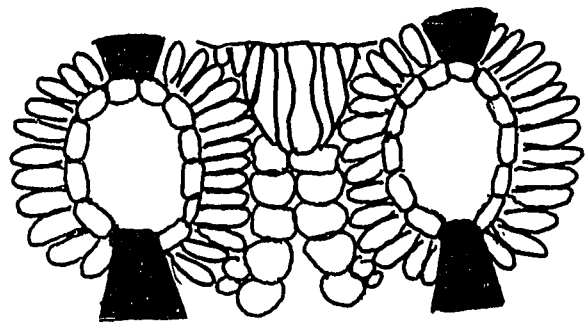

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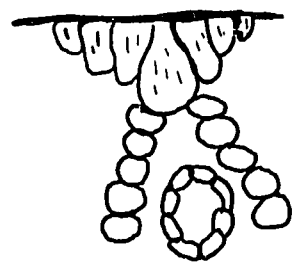
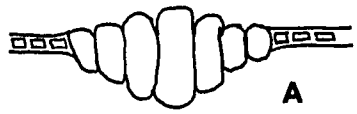


C

Figure 8. Characteristics of epidermal cells. A. Bulliform cells forming restricted groups of large and inflated cells; these bulliform cell groups projecting above the level of the epidermis. B. Bulliform cells forming restricted groups of large and inflated cells, situated at the same level that the general epidermis surface. C. Bulliform cells forming fan-shaped groups, situated at the bases of the furrows. D. Outer tangential epidermal cells thickened and covered by a distinct, thick cuticle continuous over the epidermal cells. E. Hairs thick and short, sunken between epidermal cells. F. Papillae wide, with the distal, outer wall markedly thickened



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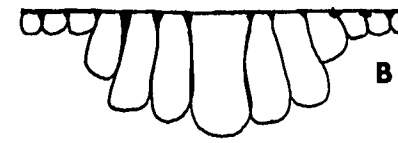

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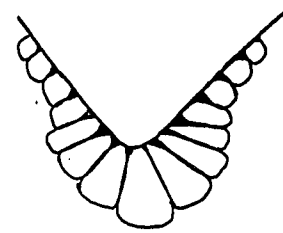

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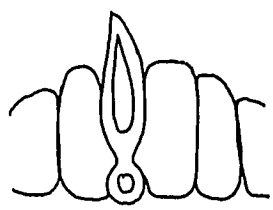


E

F

(1960), and Ellis (1979). The two surfaces of the leaf were observed. In general, the abaxial and adaxial surface appear similar, except for the presence of bulliform cells only on the adaxial surface. Only when necessary the location (abaxial or adaxial surface)of a character is pointed out.

2. General considerations

The leaf epidermal survey of Sorghastrum species using light microscopy, as well as scanning electron microscopy shows various important characters. From the results obtained the following considerations should be pointed out:

I. The stomata may be in one or more rows in each intercostal zone. The species that show only one row are: S. chaseae, S. elliottii, S. incompletum, S. nudipes. S. rigidifolium, S. scaberrimum, S. secundum, S. setosum, S. stipoides, and S. viride. The rest may show one and two rows of stomata, or as in S. pellitum, even three rows.

II. The interstomatal cells may be rectangular or square. The species that show square interstomatal cells are S. chaseae, S. rigidifolium, S. trichopus, and S. viride. In addition, S. incompletum, S. minarum, S. nudipes, S. nutans, S. scaberrimum, S. setosum, and S. stipoides show both shapes (rectangular and square). On the other hand, S. balansae, S. brunneum, S. contractum, S. elliottii, S. pellitum, and S. secundum have only rectangular interstomatal cells.

III. Papillae may be present or absent on the interstomatal cells. If present, they may be conspicuous on both leaf surfaces, or only on one of them. The only species that does not show papillae is S. balansae.

However, in some cases, slight protuberances on the interstomatal cells are observed.

IV. Within the species of Sorghastrum showing papillae, two shapes of papillae are shown: a globose shape that does not overarch the stomata, and an elongated form that overarches the stomata. The latter shape is shown by S. brunneum, S. chaseae, and S. pellitum. This last species shows a unique elongated form of papillae. The rest of the species, except S. balansae have the globose and not overarching form.

V. With respect to the shape of the intercostal short cells, the observations indicate that S. chaseae and S. incompletum have rounded cells. In addition, S. balansae, S. contractum, S. minarum, S. nudipes, S. nutans, S. pellitum, S. rigidifolium, S. scaberrimum, S. setosum, S. stipoides and S. viride show tall and narrow cells. On the other hand, S. brunneum, S. elliottii, and S. secundum show square cells. Finally, S. trichopus does not show well defined intercostal short cells.

VI. The costal short cells may be rectangular or square. The former is sometimes shown in S. incompletum var. incompletum and in S. setosum. The rest shows the typical rectangular form.

VII. The silica bodies are typically dumbbell-shaped. Usually, the middle is narrow and short, but in S. elliottii and S. trichopus silica bodies with a narrow long middle are present.

VIII. The size of the prickles in Sorghastrum species may be small (smaller than the stomata), medium (the base slightly longer than the stomata), and large (base at least twice as long as the stomata). S.

stipoides has large prickles, whereas S. minarum, S. nudipes and S. setosum show small ones. On the other hand, S. chaseae and S. incompletum show, in the same leaf epidermis, both small and medium size prickles. The rest of the species have medium size prickles.
IX. Macrohairs are shown in both surfaces by S. scaberrimum, whereas in S. chaseae, S. contractum, and S. viride they are only present on the adaxial surface.

3. Descriptions

Sorghastrum Nash

INTERCOSTAL LONG CELLS: long and narrow (three times or more longer than width) (Fig. 9A), rectangular, end walls vertical or angled in relation to the horizontal walls; cell shape relatively constant; cell size varies in single files; outline markedly sinuous, interlocking and raised; usually microhairs, seldom prickle hairs are associated; papillae lacking. STOMATA: subsidiary cells triangular or slightly dome-shaped (Fig. 9B), usually just one row of stomata is present in each intercostal zone, sometimes two or more rows, in that case the rows are adjacent to one another, not separated by files of intercostal long cells; generally abundant in the abaxial surface and less abundant at the adaxial one. INTERSTOMATAL CELLS: rectangular or square, very seldom rounded; one interstomatal cell between successive stomata; end walls fitting against the stomata slightly concave (U-shaped), the outline markedly sinuous, interlocking and raised; papillae present or absent. INTERCOSTAL SHORT CELLS: tall and narrow (vertical dimension greater than horizontal

dimension) (Fig. 9C), or square (Fig. 9D), with smooth or sinuous walls, located between successive long cells in a file. PAPILLAE: lacking or present, elongated and overarching the stomata (Figs. 9E and 9F), or globose and not overarching the stomata (Figs. 9G and 9H); thin or distinctly thickened, located in the intercostal zone, in the interstomatal cells, one papilla per cell. COSTAL SHORT CELLS: square (Fig. 9N) or rectangular (Fig. 9O), with sinuous or straight walls, diverse number of files of cells comprise the costal zone, files all similar or alternating. SILICA BODIES: located mainly throughout the costal zones, transversally elongated, dumbbell-shaped, middle narrow (Fig. 9K), ends rounded (Fig. 9L) or concave (Fig. 9M). MICROHAIRS: bicellular, located between intercostal long cells, emerging vertically of a short cell (Fig. 9J); basal and distal cells approximately equal in length, (cells five or more times as long as wide) (Fig. 9I); Basal Cell more inflated than the distal cell, length much greater than width (more than two times the width), Distal Cell wall thinner than wall of basal cell, often deciduous, length much greater than the width (more than two times the width), the apex slightly tapered or sharply pointed. PRICKLE HAIRS: lacking or present, with pointed apex and a swollen base; the base as long, shorter or longer than the stomata, barb longer or shorter than the base and always developing basally from the apex of the base (Figs. 9P, 9Q and 9R); usually located in the costal zone, seldom in the intercostal long cells, frequent (not more than 5 silica bodies between successive prickles), or infrequent (more than 5 silica bodies between succesive prickles. MACROHAIRS: lacking or present, unicellular, soft

or stiff, sometimes an specialized hemispherical epidermal cell associated with the base of the hair.

1. Sorghastrum balansae (Hackel) Davila (Fig. 10).

STOMATA: subsidiary cells tringular, two rows of stomata in each intercostal zone, abundant on the abaxial surface, and common on the adaxial one. INTERSTOMATAL CELLS: rectangular, without papillae. INTERCOSTAL SHORT CELLS: tall and narrow, smooth walls (Fig. 9C). COSTAL SHORT CELLS: square, with sinuous walls (Fig. 9N). SILICA BODIES: middle narrow and short, ends concave or rounded (Figs. 9K, 9L and 9M). PRICKLES: located on the costal zone, medium size (the base slightly longer than the stomata) (Fig. 9Q), barb equal or longer than the base, frequent (no more than 5 silica bodies between successive prickles of a file). MACROHAIRS: lacking.

Specimens examined: Chase 11919 (US); Jorgensen 4574 (MO); Macedo 2130 (US); Pedersen 3287 (US).

2. Sorghastrum brunneum Swallen (Fig. 11).

STOMATA: subsidiary cells triangular, one or two rows of stomata in each intercostal zone, abundant on the abaxial face, and common on the adaxial one. INTERSTOMATAL CELLS: rectangular, papillae present at the abaxial surface, but absent on the adaxial one. INTERCOSTAL SHORT CELLS: square, with smooth walls (Fig. 9D). PAPILLAE: elongated and overarching the stomata (Fig. 9F). COSTAL SHORT CELLS: square, with sinuous walls (Fig. 9N). SILICA BODIES: middle short and narrow, ends concave or rounded (Figs. 9K, 9L and 9M). PRICKLES: located on the

costal zone, medium size (the base slightly longer than the stomata) (Fig. 9Q), barb shorter than the base, frequent (not more than 5 silica bodies between successive prickles of a file), abundant on the abaxial surface, scattered on the adaxial one. MACROHAIRS: lacking. Specimens examined: Johnston 6024 (LL); Molina & Molina 27628 (ENCB); Pohl & Davidse 12139 (ISC); Rzedowski 121159 (ENCB); Steyermark 31325 (F); Ventura 4465 (ENCB).

3. Sorghastrum chaseae Swallen (Figs. 12 and 13).

STOMATA: subsidiary cells triangular, one row of stomata in each intercostal zone, abundant. INTERSTOMATAL CELLS: square, with papillae. INTERCOSTAL SHORT CELLS: rounded, smooth walls. PAPILLAE: on the abaxial surface, elongated and overarching the stomata (Fig. 9E); on the adaxial surface, globose and not overarching the stomata (Fig. 9H). COSTAL SHORT CELLS: square, with sinuous walls (Fig. 9N). SILICA BODIES: middle short and narrow, ends rounded or concave (Figs. 9K, 9L and 9M). PRICKLES: located on the costal zone, First type medium size (slightly longer than the stomata) (Fig. 9Q), barb as long as the base, frequent (less than 5 silica bodies between successive prickles of a file); Second type small size (smaller than the stomata) (Fig. 9P), barb shorter than the base, infrequent (more than 5 silica bodies between successive prickles), this last type is located on the intercostal zone, in the interstomatal cells. MACROHAIRS: not present on the abaxial surface, but quite common on the adaxial one, in the intercostal zone, with raised epidermal cells at the base.

Specimens examined: Chase 1644 (US); Chase 11861 (US).

4. Sorghastrum contractum (Hackel) Kuhlm. and Kuhn (Figs. 14 and 15).

STOMATA: subsidiary cells triangular or slightly dome-shaped, one or two rows of stomata in each intercostal zone, abundant. INTERSTOMATAL CELLS: rectangular, papillae present on the abaxial surface, but absent on the adaxial one. INTERCOSTAL SHORT CELLS: tall and narrow, straight walls (Fig. 9C). PAPILLAE: on the abaxial surface globose and not overarching the stomata (Fig. 9G); on the adaxial surface lacking. COSTAL SHORT CELLS: square, with sinuous walls (Fig. 9N). SILICA BODIES: middle short and narrow, ends rounded (Figs. 9K and 9L). PRICKLES: located on the costal zone of the abaxial surface, lacking on the adaxial surface, medium size (the base slightly longer than the stomata) (Fig. 9Q), barb equal or longer than the base, infrequent (more than 5 silica bodies between successive prickles of a file). MACROHAIRS: lacking on the abaxial surface, but present on the adaxial one, in the intercostal zone, infrequent, with raised epidermal cells at the base. Specimens examined: Chase 8723, 10898 (US); Holway & Holway 1499(US); Goodland & Maycock 499 (NY).

5. Sorghastrum elliottii (Mohr) Nash (Fig. 16).

STOMATA: subsidiary cells triangular, one row of stomata in each intercostal zone, abundant. INTERSTOMATAL CELLS: rectangular, papillate. INTERCOSTAL SHORT CELLS: square with smooth walls (Fig. 9D). PAPILLAE: globose, not overarching the stomata (Fig. 9H). COSTAL SHORT CELLS: square with smooth walls (Fig. 9N). SILICA BODIES: middle short or long and narrow, ends concave (Figs. 9K and 9M). PRICKLES: located

on the costal zone, medium size (the base slightly longer than the stomata) (Fig. 9Q), barb shorter than the base, frequent (not more than 5 silica bodies between successive prickles of a file. MACROHAIRS: lacking.

Specimens examined: Blomquist 9859 (F); Chapman 4639 (NY); Godfrey 76630 (MO); Kearney 942 (US); King 2205 (TEX); York s.n. (MO).

6. Sorghastrum incompletum (Presl) Nash (Fig. 17).

STOMATA: subsidiary cells triangular, one row of stomata in each intercostal zone, abundant on the abaxial surface, sometimes infrequent on the adaxial one. INTERSTOMATAL CELLS: square on the abaxial surface and usually rectangular on the adaxial one; papillate on both surfaces, or only on the abaxial one. INTERCOSTAL SHORT CELLS: rounded. PAPILLAE: globose, not overarching the stomata (Fig. 9H). COSTAL SHORT CELLS: in var. incompletum generally rectangular (Fig. 9O) and in var. bipennatum square (Fig. 9N). SILICA BODIES: middle narrow and short, ends rounded (Figs. 9K and 9L). PRICKLES: located on the costal zone; in var. incompletum medium size (base slightly longer than the stomata) (Fig. 9Q), infrequent (more than 5 silica bodies between successive prickles of a file); in var. bipennatum small (base shorter than the stomata) (Fig. 9P), frequent (no more than 5 silica bodies between successive prickles of a file). MACROHAIRS: lacking.

Specimens examined: Baptista 14175 (US); Breedlove & Raven 13380 (US); Davila et al. 194, 196. 206, 207 (ISC); Davidse 3138 (VEN); Gossweiler s.n. (US); McVaugh 20202 (NY); Pohl & Davidse 11396 (ISC); 11589 (F).

7. Sorghastrum minarum (Nees) Hitchcock (Fig. 18).

STOMATA: subsidiary cells triangular, one or two rows of stomata in each intercostal zone, abundant. INTERSTOMATAL CELLS: square or seldom rectangular, papillate only on the abaxial surface. INTERCOSTAL SHORT CELLS: tall and narrow, with smooth walls (Fig. 9C). PAPILLAE: globose, not overarching the stomata (Fig. 9G). COSTAL SHORT CELLS: square, with straight walls (Fig. 9N). SILICA BODIES: middle narrow and short, ends concave (Figs. 9K and 9M). PRICKLES: located on the costal zone of the abaxial surface, sometimes on the adaxial surface in the intercostal zone; small (base shorter than the stomata) (Fig. 9P), barb shorter than the base, infrequent (more than 5 silica bodies between successive prickles of a file). MACROHAIRS: lacking.

Specimens examined: Chase 10870 (F); Davidse & Ramamoorthy 10627 (MO); Pederson 1033 (US); Quarin et al. 2233 (US); Schinnini 6537 (CTES); Smith & Klein 12216 (NY, US).

8. Sorghastrum nudipes Nash (Fig. 19).

STOMATA: subsidiary cells triangular, one row of stomata in each intercostal zone, abundant. INTERSTOMATAL CELLS: square or seldom rectangular, papillate. INTERCOSTAL SHORT CELLS: tall and rounded, with smooth walls (Fig. 9C). PAPILLAE: globose, without overarching the stomata (Fig. 9H). COSTAL SHORT CELLS: square, with sinuous walls (Fig. 9N). SILICA BODIES: midddle narrow and short, ends rounded (Figs. 9K and 9L). PRICKLES: located on the costal zone, small (base shorter than the stomata) (Fig. 9P), barb shorter than the base, frequent (less than 5 silica bodies between successive prickles of a file). MACROHAIRS:

lacking.

Specimens examined: Davila et al. 137, 142. 143 (ISC); Palmer 11 (US); Pringle 1433 (US); Siqueiros 1616 (COT); Tenorio et al. 9968, 10085 (MEXU).

9. Sorghastrum nutans (L.) Nash (Fig. 20).

STOMATA: subsidiary cells triangular, one or two rows of stomata in each intercostal zone, abundant. INTERSTOMATAL CELLS: square or seldom rectangular, papillate. INTERCOSTAL SHORT CELLS: tall and narrow, with smooth walls (Fig. 9C). PAPILLAE: globose, without overarching the stomata (Fig. 9H). COSTAL SHORT CELLS: square with sinuous walls (Fig. 9N). SILICA BODIES: middle narrow and short, ends rounded (Figs. 9K and 9L). PRICKLES: located on the costal zone, medium size (base slightly longer than the stomata) (Fig. 9Q), barb shorter than the base, frequent (less than 5 silica bodies between successive prickles of a file). MACROHAIRS: lacking.

Specimens examined: Beetle M-5809 (COT); Guerrero 425 (COT); Johnston 5926 (US); Johnston 7099 (LL); Jones s.n. (F); Kearney 294 (US); McDonald s.n. (NY); Moran 5864 (US); Patterson 536 (LL); Purpus 2897 (US); Rzedowski 3591 (ENCB); Small s.n. (F).

10. Sorghastrum pellitum (Hackel) Parodi (Figs. 21 and 22).

STOMATA: subsidiary cells triangular, one to three rows of stomata in each intercostal zone, abundant. INTERSTOMATAL CELLS: rectangular, papillate. INTERCOSTAL SHORT CELLS: tall and narrow, smooth walls (Fig. 9C). PAPILLAE: very elongated and truncate at the top, overarching the

stomata (Fig. 9E). COSTAL SHORT CELLS: square, with sinuous walls (Fig. 9N). SILICA BODIES: middle narrow and short, ends concave (Figs. 9K and 9M). PRICKLES: located on the costal zone, medium size (the base slightly longer than the stomata) (Fig. 9Q), barb shorter than the base, frequent (not more than 5 silica bodies between successive prickles). MACROHAIRS: lacking.

Specimens examined: Cano 4510 (BAB); Clos & Molfino 259 (BAB); unziker 4535 (BAB); Montes 15252 (SI); Pedersen 6064 (MO); Schinini & Carnevalli 10411 (CTES); Reitz & Klein 5347 (US).

11. Sorghastrum rigidifolium (Stapf) Chippindall (Fig. 23).

STOMATA: subsidiary cells triangular, one row of stomata in each intercostal zone, abundant. INTERSTOMATAL CELLS: square, without papillae on the abaxial surface and showing a not well formed papillae on the adaxial one. INTERCOSTAL SHORT CELLS: tall and narrow, smooth walls (Fig. 9C). PAPILLAE: slightly globose, without overarching the stomata (Fig. 9G). COSTAL SHORT CELLS: square, sinuous walls (Fig. 9N). SILICA BODIES: middle narrow and short, ends concave (Figs. 9K and 9M). PRICKLES: located on the intercostal zone, medium size (base longer than the stomata) (Fig. 9Q), barb shorter than the base, infrequent (more than 5 silica bodies between successive cells). MACROHIARS: lacking.

Specimens examined: Ekman s.n. (LL); Greenway & Rawlines 9376 (US); Richards 17686 (MO); Vesey & Fitzgerald 3218 (MO); Wright 3896 (NY).

12. Sorghastrum scaberrimum (Nees) Herter (Figs. 24 and 25).

STOMATA: subsidiary cells triangular, one row of stomata in each intercostal zone, abundant. INTERSTOMATAL CELLS: square, seldom

rectangular, papillate on the abaxial surface, non-papillate on the adaxial one. INTERCOSTAL SHORT CELLS: tall and narrow, straight walls (Fig. 9O). PAPILLAE: globose and not overarching the stomata (Fig. 9H). COSTAL SHORT CELLS: square, with straight walls (Fig. 9N). SILICA BODIES: middle narrow and short, ends concave (Figs. 9K and 9M). PRICKLES: located on the costal zone, medium size (base slightly longer than the stomata) (Fig. 9Q), barb shorter than the base, frequent (not more than 5 silica bodies between successive prickles of a file). MACROHAIRS: common, with raised epidermal cells at the base.
Specimens examined: Chase 9841 (MO), 11579 (US); Dombrowski 9595 (ISC); Reitz & Klein 10794 (US); Smith & Klein 16073 (US).

13. Sorghastrum secundum (Elliott) Nash (Fig. 26).

STOMATA: subsidiary cells triangular, one row of stomata in each intercostal zone, abundant on the abaxial surface, infrequent on the adaxial one. INTERSTOMATAL CELLS: rectangular, papillate. INTERCOSTAL SHORT CELLS: square, with smooth walls (Fig. 9D). PAPILLAE: globose, without overarching the stomata (Fig. 9H). COSTAL SHORT CELLS: square, with straight walls (Fig. 9N). SILICA BODIES: middle narrow and short, ends rounded (Figs. 9K and 9L). PRICKLES: located on the costal zone, medium size (the base slightly longer than the stomata) (Fig. 9Q), barb shorter than the base, frequent (not more than 5 silica bodies between successive prickles of a file. MACROHAIRS: lacking.
Specimens examined: Clos 170 (US); Combs 1193 (US); Correll & Correll 52757 (NY); Curtiss 4019 (NY); Duncan 20663 (F); Nash 753 (NY).

14. Sorghastrum setosum (Grisebach) Hitchcock (Fig. 27).

STOMATA: subsidiary cells triangular, one row of stomata in each intercostal zone, abundant on the abaxial surface, common on the adaxial one. INTERSTOMATAL CELLS: rectangular or square, papillate on the adaxial surface, non-papillate on the abaxial one. INTERCOSTAL SHORT CELLS: tall and narrow, outline smooth (Fig. 9C). PAPILLAE: globose, not overarching the stomata (Fig. 9H). COSTAL SHORT CELLS: rectangular, same width as intercostal long cells (Fig. 9O). SILCIA BODIES: middle narrow and short, ends rounded (Figs. 9K and 9L). PRICKLES: lacking on the abaxial surface, present on the adaxial one, at the costal zone, small size (samller than the stomata) (Fig. 9P), barb shorter than the base, infrequent (more than 5 silica bodies between successive prickles). MACROHAIRS: lacking.

Specimens examined: Ahumada et al. 1514 (CTES); Ahumada 1622 (CTES);Conrad & Conrad 2960 (ISC); Davila et al. 205 (ISC); Davidse & Huber 14949 (MO); Irwin et al. 14553 (NY); Krapovickas et al. 24962 (CTES); Steinbach 5428 (US).

15. Sorghastrum stipoides (HBK) Nash (Fig. 28).

STOMATA: subsidiary cells triangular, one row of stomata in each intercostal zone, abundant on the abaxial surface, common on the adaxial one. INTERSTOMATAL CELLS: square or seldom rectangular, papillate. INTERCOSTAL SHORT CELLS: tall and narrow (Fig. 9C). PAPILLAE: globose and not overarching the stomata (Fig. 9H). COSTAL SHORT CELLS: square, with sinuous walls (Fig. 9N). SILICA BODIES: middle narrow and short, ends concave (Figs. 9K and 9M). PRICKLES: located on the costal zone,

large size (base at least twice as ong as stomata) (Fig. 9R), barb shorter than the base, frequent (with less than 5 silica bodies between successive prickles of a file). MACROHAIRS: lacking.
Specimen examined: Asplund 6638 (US); Hatschback 15242 (F); Hunziker 1794 (BAB); Mexia 5542 (MO); Reitz & Klein 7732 (US); Schulz 925 (MO).

16. Sorghastrum trichopus (Stapf) Pilger (Fig. 29).

STOMATA: subsidiary cells triangular, one or two rows of stomata on the intercostal zones, abundant on the abaxial surface, common on the adaxial one. INTERSTOMATAL CELLS: square, seldom rectangular, papillate. INTERCOSTAL SHORT CELLS: lacking. PAPILLAE: globose, not overarching the stomata (Fig. 9H). COSTAL SHORT CELLS: square, with straight walls (Fig. 9N). SILICA BODIES: First type with a middle narrow and long (Fig. 9K); Second type with a middle narrow and short (Fig. 9K), ends rounded (Fig. 9L). PRICKLES: located on the costal zone, medium size (base as long as stomata) (Fig. 9Q), barb shorter than the base, infrequent (with more than five silica bodies between successive prickles of a file). MACROHAIRS: lacking.
Specimens examined: Ellis 2680 (MO); Gonde 32/74 (MO); Robinson 18906 (NY) Smook & Russell 1957 (MO).

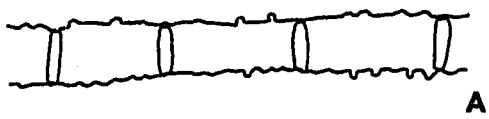
17. Sorghastrum viride Swallen (Figs. 30 and 31).

STOMATA: subsidiary cells triangular, one row of stomata in each intercostal zone, abundant on the abaxial surface, scarce on the adaxial one. INTERSTOMATAL CELLS: square, papillate. INTERCOSTAL SHORT CELLS: tall and narrow, smooth walls (Fig. 9C). PAPILLAE: slightly globose,

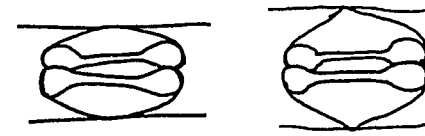
not overarching the stomata (Fig. 9G). COSTAL SHORT CELLS: square, sinuous walls (Fig. 9N). SILICA BODIES: middle narrow and short, ends rounded (Fig. 9K and 9L). PRICKLES: located on the costal zone, medium size (slightly longer than the stomata) (Fig. 9Q), barb shorter than the base, frequent (not more than 5 silica bodies between successive prickles of a file). MACROHAIRS: lacking on the abaxial surface, but present on the adaxial one, with raise epidermal cells at the base.

Specimens examined: Burkart & Troncoso 26202 (SI); Hassler 11075 (US); Morong 547 (NY); Quarin 417 (SI); Rosengurtt B-8433 (US); Trescens 2654 (CTES).

Figure 9. Some important epidermal features. A. Intercostal long cells elongated, with sinuous and undulated walls. B. Subsidiary cells of the stomata triangular. C. Intercostal short cells tall and narrow. D. Intercostal short cells square. E. Papillae completely overarching the stomata. F. Papillae partially overarching the stomata. G. Papillae globose and slightly thickened. H. Papillae globose and strongly thickened. I. Microhairs with the basal and distal cells approximately the same length; basal cell more inflated than distal cell. J. Microhairs emerging straight out of a short cell. K. Silica bodies with a narrow central or middle portion. L. Silica bodies with rounded ends. M. Silica bodies with concave or indented ends. N. Costal short cells square. O. Costal short cells rectangular. P. Prickle hairs small (base shorter than the stomata). Q. Prickle hairs medium (base as long or slightly longer than the stomata). R. Prickle hairs large (base at least twice as long as the stomata)



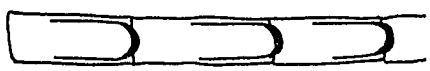
A



B

C

D



E

F

G

H

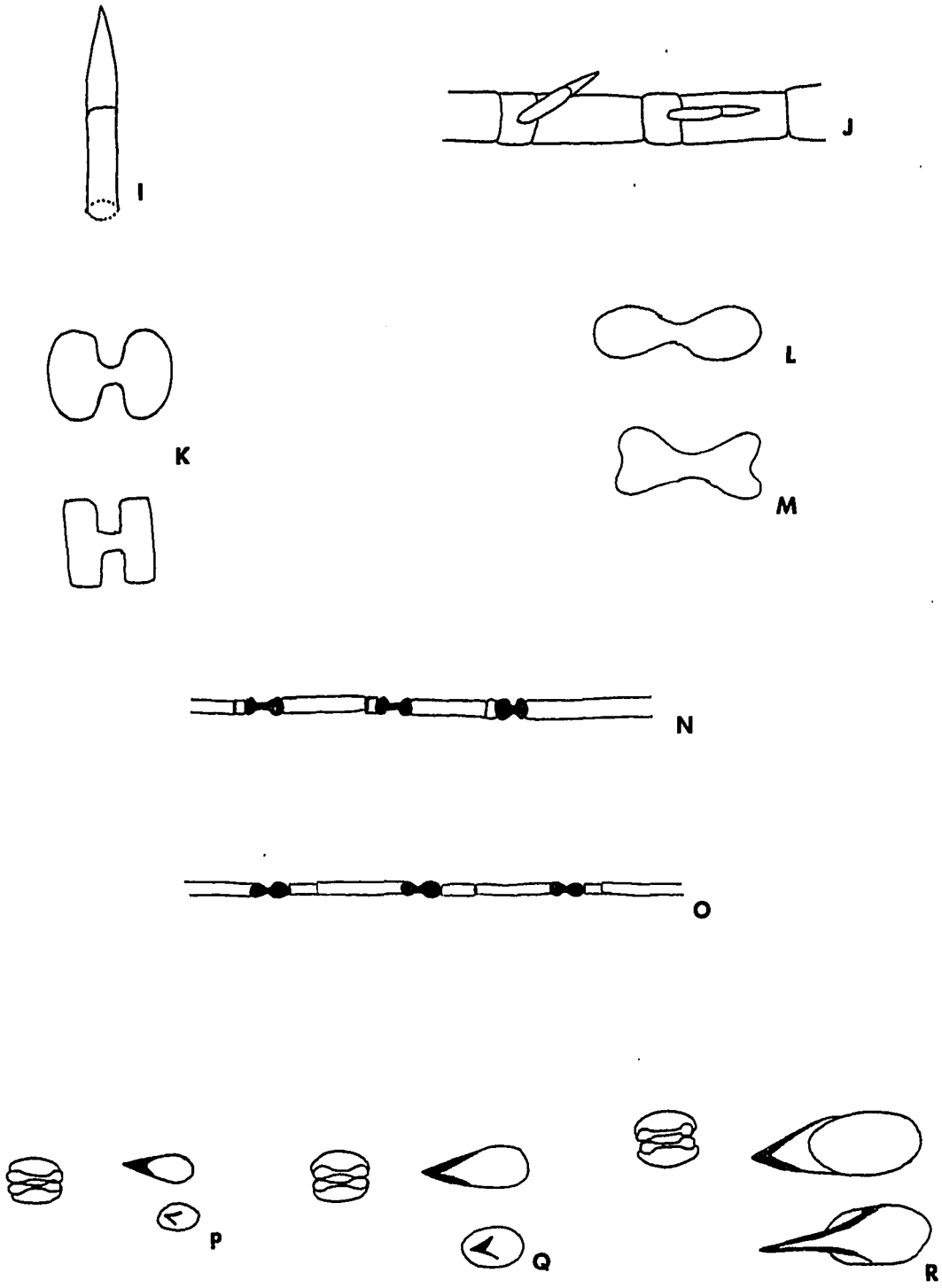


Figure 9 (Continued)

Figures 10-12. Abaxial leaf epidermal views of selected Sorghastrum species, bar=20 um

Figure 10. Sorghastrum balansae (Chase 11919)
Figure 11. Sorghastrum brunneum (Johnston 6024)
Figure 12. Sorghastrum chaseae (Chase 11861)

Figure 13. Adaxial leaf epidermal view of Sorghastrum chaseae (Chase 11861) showing macrohairs, bar=50 um

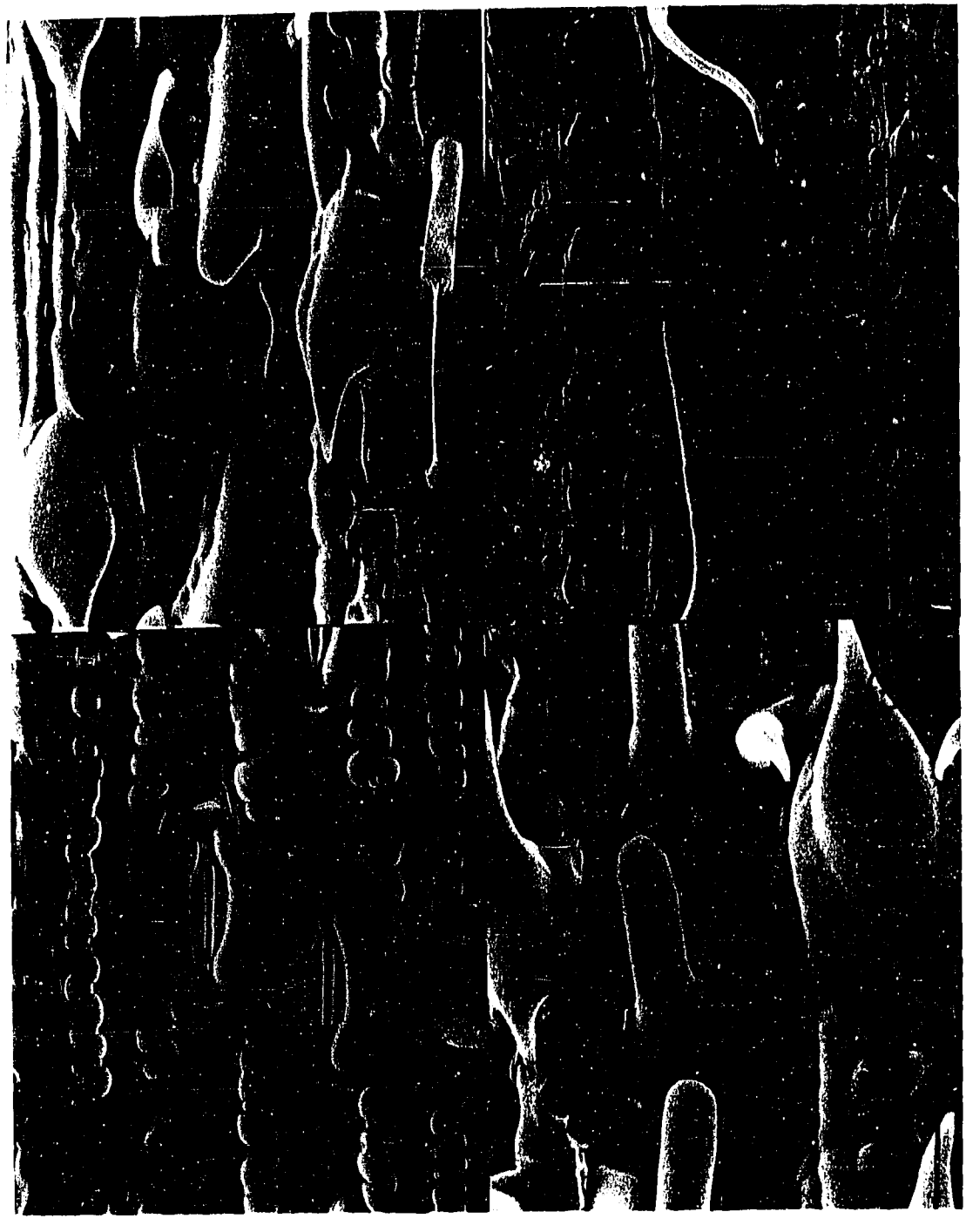


Figure 14. Adaxial leaf epidermal view of Sorghastrum contractum (Chase 8723)

Figures 15-17. Abaxial leaf epidermal views of selected Sorghastrum species, bars=20 um

Figure 15. Sorghastrum contractum (Chase 8723)
Figure 16. Sorghastrum elliottii (Kearney 942)
Figure 17. Sorghastrum incompletum (Pohl 11589)

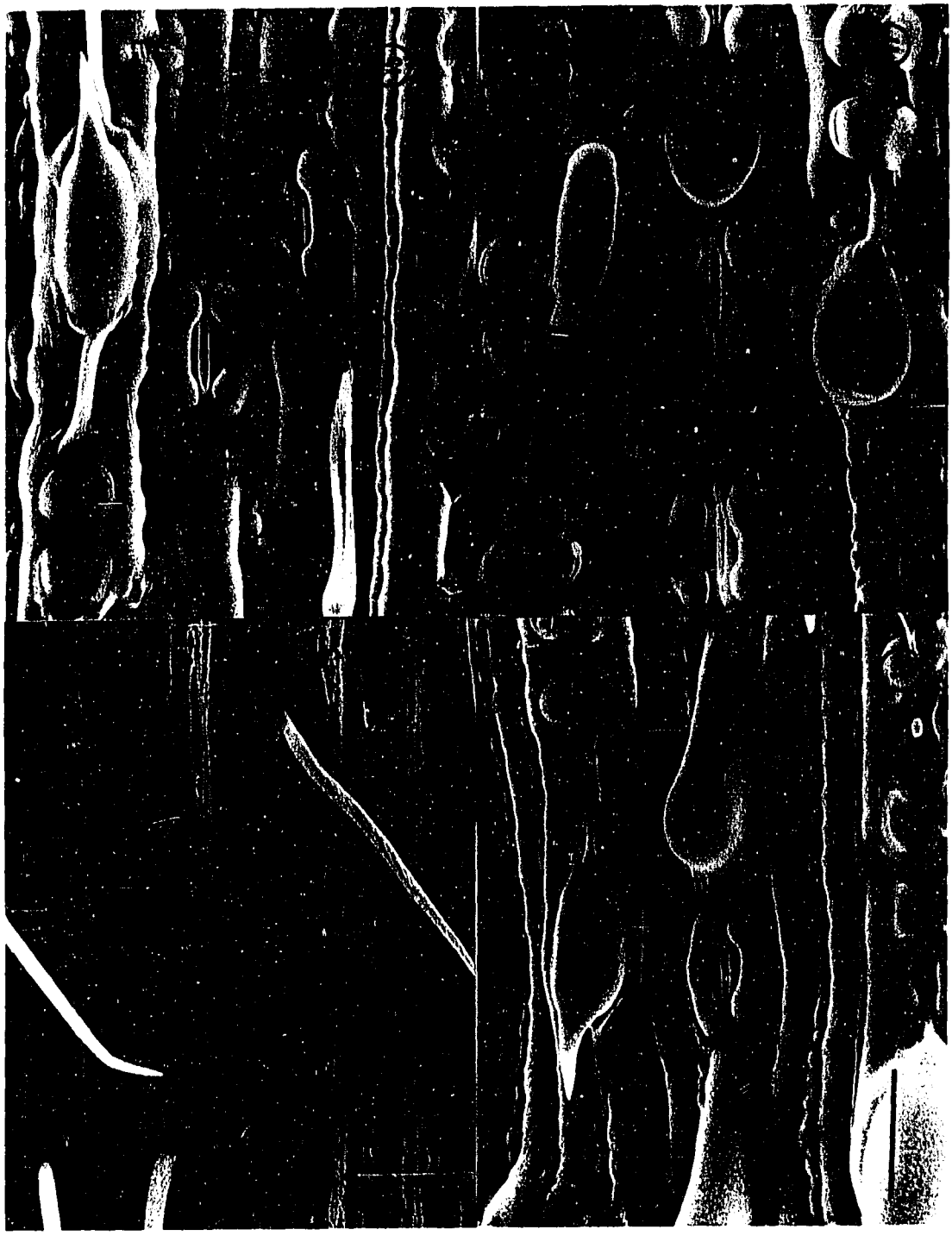


Figure 18-20. Abaxial leaf epidermal views of selected Sorghastrum species, bars=20 um

Figure 18. Sorghastrum minarum (Chavez 587)
Figure 19. Sorghastrum nudipes (Pringle 1433)
Figure 20. Sorghastrum nutans (Small s.n.)

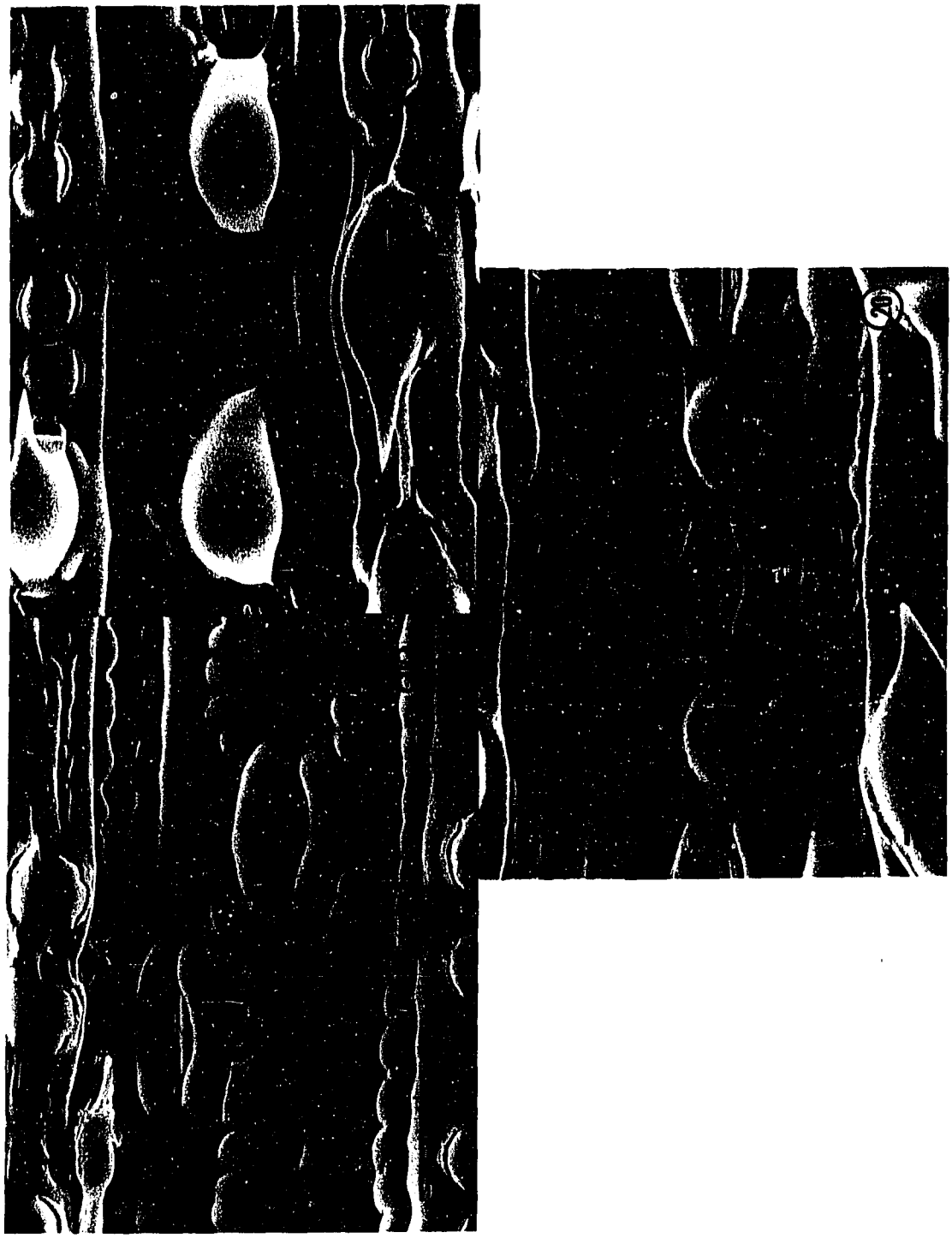


Figure 21. Abaxial leaf epidermal view of Sorghastrum pellitum (Cano 4510), bar=50 um

Figures 22-23. Abaxial leaf epidermal view of selected Sorghastrum species, bars=20 um

Figure 22. Sorghastrum pellitum (Cano 4510)
Figure 23. Sorghastrum rigidifolium (Greenway & Rawlines 9376)

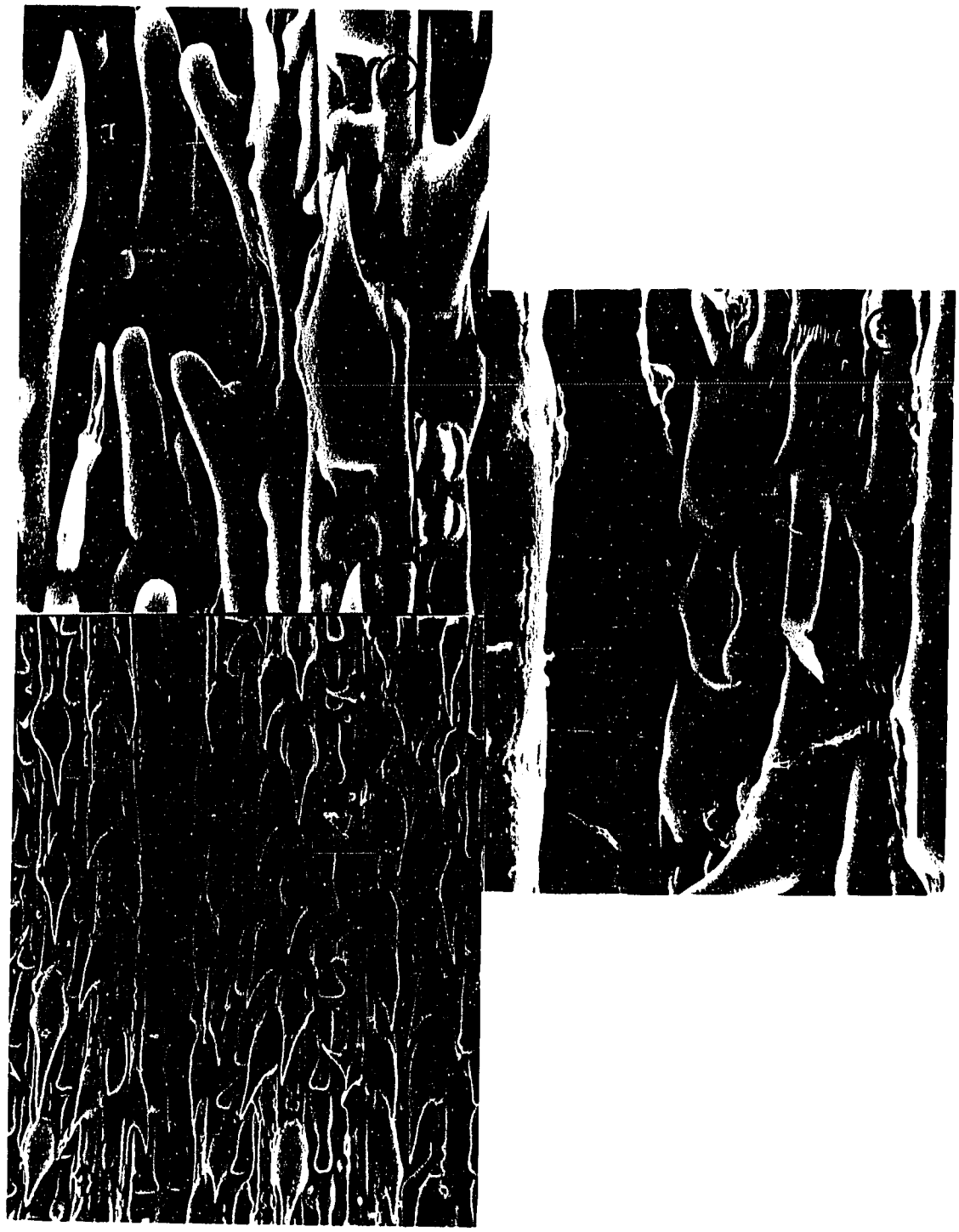
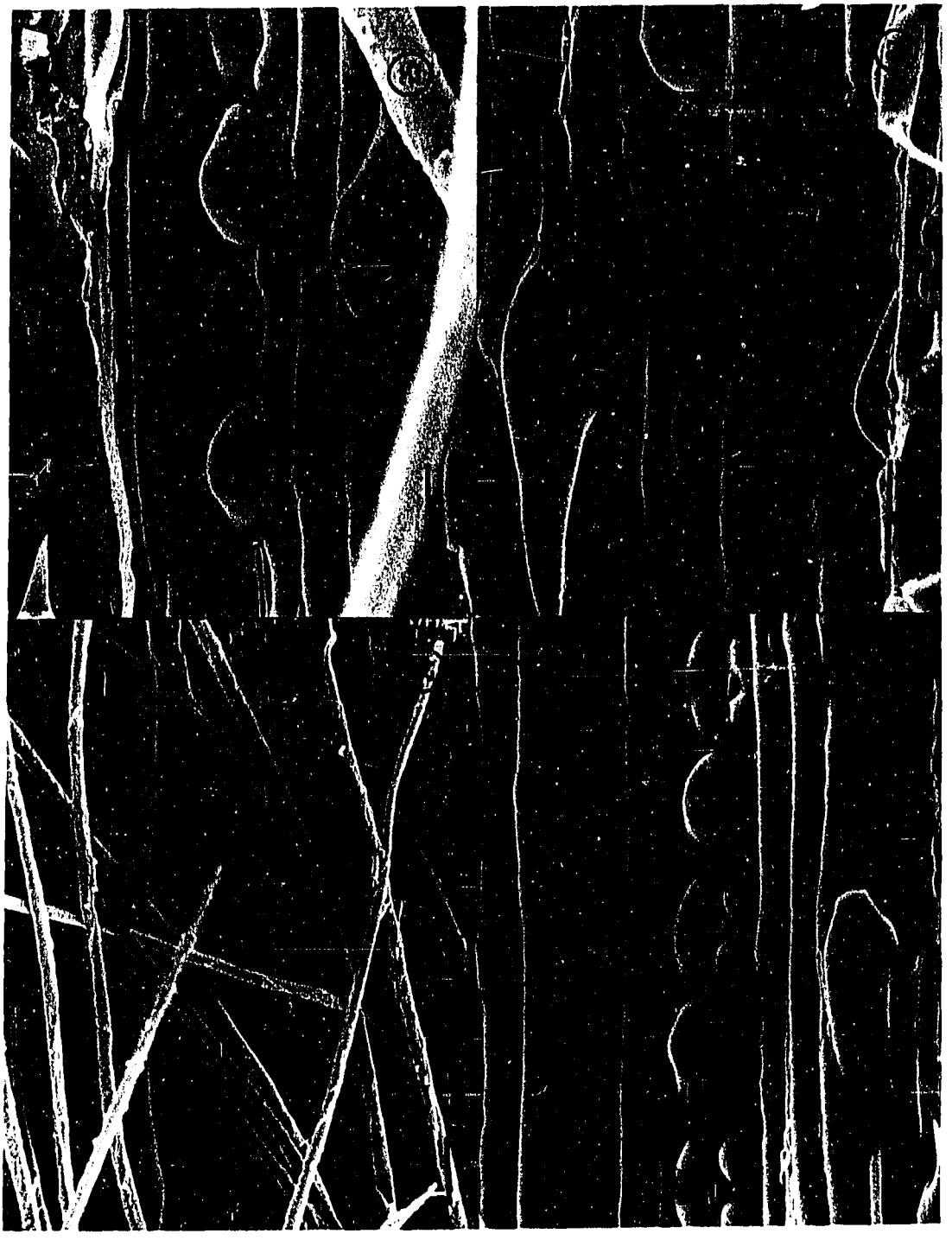


Figure 24. Adaxial leaf epidermal view of Sorghastrum scaberrimum (Chase 11579) showing macrohairs, bar=50 um

Figures 25-27. Abaxial leaf epidermal views of selected Sorghastrum species, bars=20 um

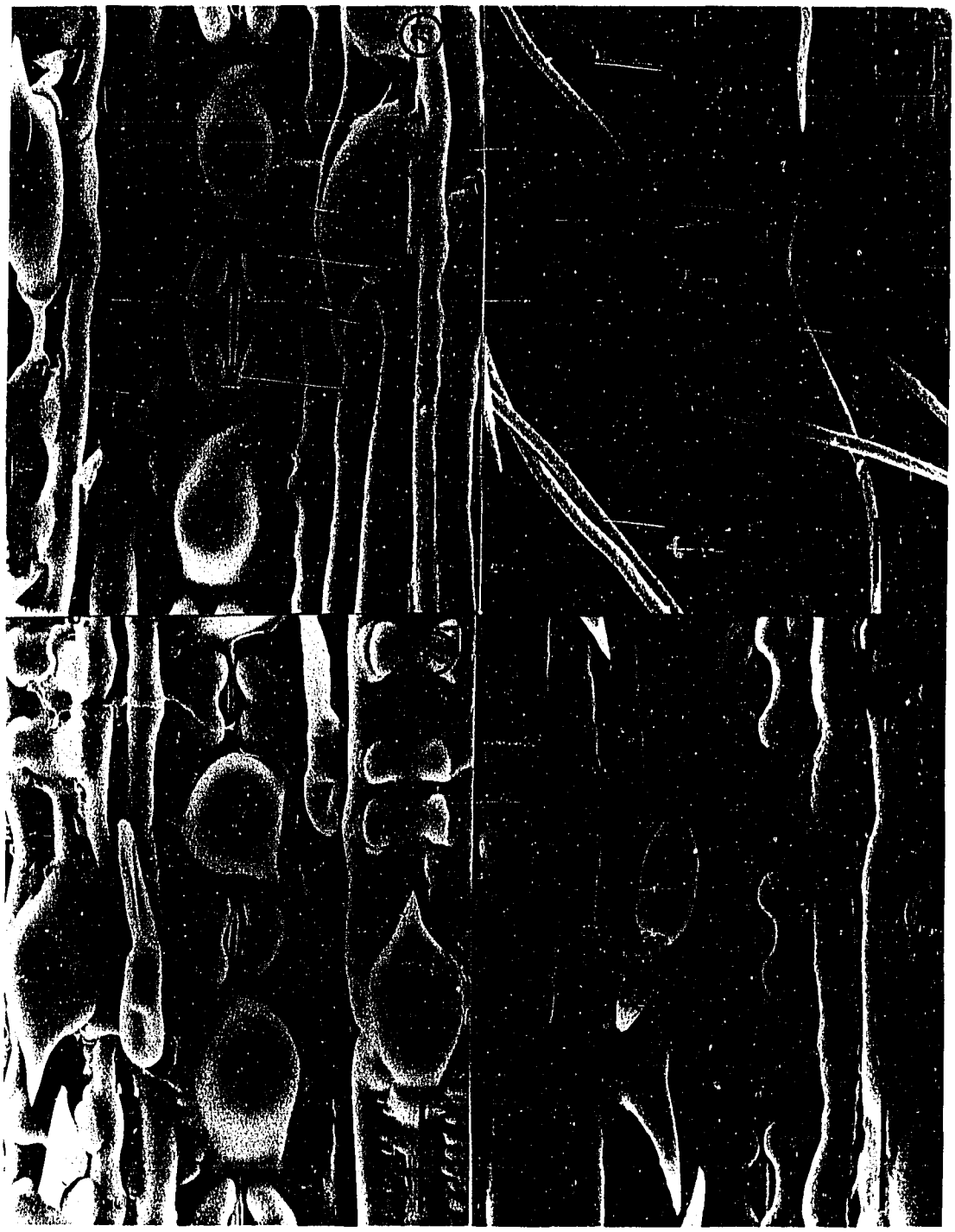
Figure 25. Sorghastrum scaberrimum (Chase 11579)
Figure 26. Sorghastrum secundum (Duncan 20663)
Figure 27. Sorghastrum setosum (Ahumada 1622)



Figures 28-30. Abaxial leaf epidermal views of selected Sorghastrum species, bars=20 um

Figure 28. Sorghastrum stipoides (Mexia 5542)
Figure 29. Sorghastrum trichopus (Robinson 18906)
Figure 30. Sorghastrum viride (Trescens 2654)

Figure 31. Adaxial leaf epidermal view of Sorghastrum viride (Trescens 2654) showing macrohairs, bar=50 um



VIII. SYSTEMATICS

A. Taxonomic History of Sorghastrum

It is generally recognized that the Andropogoneae is, in general terms, a well defined taxonomic entity. However, at the generic level the delimitations are very difficult and in many cases very obscure. This is due probably to great morphological modification of the pedicelled spikelet and consequent reduction in inflorescence branches.

Among all these problematic genera, the genus Sorghastrum has been a taxon with an uncertain and changeable taxonomic status. This genus comprises 17 species native to either Africa or the Americas. There is no previous monographic treatment of Sorghastrum. However, several authors, at different times, suggested diverse names, as well as various taxonomic ranks.

The taxonomic history of the species presently included in Sorghastrum may be said to begin with the work of Trinius (1820). In "Fundamenta Agrostographiae", he proposed the genus Chrysopogon. His description is so general that it may be applied to Sorghastrum, as well as many other Andropogoneae genera. This author mentioned the existence of spikelets arranged in triads, which is frequent at the tips or/and basal parts of Sorghastrum inflorescence. In addition, he described a sessile spikelet with two florets; one reduced and represented by a hyaline bract and the second one fertile, formed by two hyaline bracts, one of which is awned. This character fits with Sorghastrum, as well as with other related genera such as Sorghum and Andropogon. Finally,

Trinius described the two lateral spikelets (pedicelled) as being reduced to two hyaline awnless bracts. In many species of Sorghum those two reduced bracts are commonly present. On the other hand, in Sorghastrum at times, two reduced bracts supported by the pedicel may be shown in the spikelets located in the basal and uppermost zones of the inflorescence. In summary, the genus Chrysopogon is in part a synonym of the genus Sorghastrum.

Rafinesque (1830) was the first to recognize this genus as a separate entity. This author proposed the Name Poranthera. However, this name is a homonym of Poranthera Rudge published in 1811 for a different genus. Based on priority (Art. 11.2-ICBN), Rafinesque's name must be rejected.

In 1881, Bentham mentioned that the genera Chrysopogon and Sorghum were closely related. He mentioned that the former was a genus comprising nearly 20 species, chiefly tropical and subtropical, but including also some temperate species, such as the European Chrysopogon gryllus (=Andropogon gryllus). Bentham divided the genus Chrysopogon into two "natural" sections. The typical one, section Chrysopogon, in which the pedicellate spikelets usually contain a male flower, and the section Stipoides, exclusively American, in which reduced hairy stipes, rarely bearing a rudimentary glume, are present. This latter section represents a synonym of the genus Sorghastrum.

Fournier (1881) included the genus Sorghastrum within Andropogon section Sorghastrum. The author separated the section Sorghastrum from

the others by its paniculate inflorescence. However, with all the information available it seems unreasonable to retain Fournier's point of view. It is currently accepted (Celarier 1959, Clayton and Renvoize 1986) that Andropogon and Sorghastrum represent probably two different evolutionary lines in the Andropogoneae.

Hackel (1883) included many Sorghastrum species as subspecies and varieties of Sorghum nutans section Chrysopogon. This author cited 7 subspecies and 7 varieties that correspond in this treatment to 7 of the 17 recognized species of Sorghastrum (Sorghastrum contractum, S. elliottii, S. nutans, S. pellitum, S. scaberrimum, S. setosum, and S. stipoides). In addition to this complex species Sorghum nutans, Hackel cited the species Sorghum minarum and Sorghum canescens that currently correspond to Sorghastrum minarum and Sorghastrum incompletum respectively.

In 1889, Hackel transferred his former genus Sorghum, section Chrysopogon into the genus Andropogon subgenus Sorghum. Analogous to his former treatment, the author suggested Andropogon nutans as having 9 varieties and 3 subvarieties, which correspond to the same current species mentioned in the previous paragraph. In addition, Hackel mentioned Andropogon unilateralis (Sorghastrum secundum), Andropogon balansae (Sorghastrum balansae), Andropogon minarum (Sorghastrum minarum), and Andropogon bipennatus (Sorghastrum incompletum var. bipennatum).

It is obvious that Hackel did not understand the genus Sorghastrum as one taxonomic entity and consequently in both of his treatments he

separated the current species of Sorghastrum in two groups. The first group (the subspecies and varieties of Sorghum nutans, or the varieties and subvarieties of Andropogon nutans) is represented by the species that show small awns (3 cm or less). The second group (the different species already mentioned belonging to the genera Sorghum and Andropogon) is represented by the species that show long awns (more than 3 cm). Besides being a very artificial separation of taxa, it is hard to conceive a species that shows so many subspecies or varieties.

Nash (1901) recognized the present genus as a different taxonomic entity from Sorghum and Andropogon. He suggested the new name Sorghastrum which means "poor imitation of the genus Sorghum". Following the rules of nomenclature, this name is legitimate and the former and latter suggested names should be considered synonyms of this genus. In the North America Flora, Nash mentioned 7 species that correspond respectively to the current species Sorghastrum elliottii, S. nudipes, S. nutans, S. incompletum, D. secundum and S. setosum.

Lunell (1915) rejected the genus Sorghastrum because of its "cheap" and "undesirable" meaning. Furthermore, he suggested the new name Chalcoelytrum which means "copper husks", making reference to the golden aspect of its spikelets. However, Lunell's point of view does not have any nomenclatural basis, and Chalcoelytrum should also be considered another synonym of Sorghastrum.

Once Nash's transference took place, most of the American agrostologists followed it. However, Stapf (1919) in Flora of Tropical

Africa, proposed the inclusion of Nash's genus as the section Sorghastrum of the genus Sorghum. He included 6 African species that currently correspond to Sorghastrum incompletum var. bipennatum, Sorghastrum rgidifolium, and Sorghastrum trichopus. However, even though Sorghastrum is related to Sorghum they are considered separated taxonomic entities and consequently Stapf's name should be also considered a synonym of Sorghastrum.

Finally, based on a cytotaxonomic study, (Garber, 1950) proposed the inclusion of the present genus in Andropogon subgenus Sorghastrum. Garber's decision is based only in the analysis of cytological characteristics of the Sorghastreae. However, it is by no means acceptable to make taxonomic decisions based on unique characters, or incomplete character information.

B. Cladistic Analysis

One of the main objectives of plant systematists is to obtain a reasonable phylogenetic estimate of the taxon or taxa that are being studied. Although it may be almost impossible to achieve a perfect phylogenetic historic review of the group, a phylogenetic approach based on the updated data should be important and useful.

Independently of the methodology used, after a better knowledge of the group is available due to accumulation of new information, all the premises and assumptions proposed within any phylogenetic philosophy might be changed or even deleted. The only fact that should remain

unchangeable regardless of the philosophic point of view chosen, is the need of an integrated and deep knowledge of the group of interest. There is no sense in carrying out a phylogenetic estimation of a taxon if it is not well documented first.

Different phylogenetic approaches have been developed during the last twenty years. One of these, cladistics, is concerned with the concepts and methods of assessing phylogenetic relationships, and especially with the production of phylogenetic trees (Funk and Stuessey, 1978).

Many different cladistic approaches have been developed. Among all of them, the one proposed by Hennig (1950, 1966), was chosen for this phylogenetic analysis. This method requires the determination of primitive and derived character states. This means that assumptions dealing with "primitiveness" and "advancement" within each character state, have to be carried out based on all the available data. Some of the disadvantages concerning this method are that generally hybridization is not identified (Combs et al. 1981). Also, reticulate and parallel evolution cannot be easily detected or graphically demonstrated (Sneath, 1975).

The characters chosen in this analysis are those determined to be distinctive to certain species or species groups. Their polarization is based on assumptions taken from what is known within the Gramineae, the Andropogoneae, and especially on the information obtained in this work. Although the adaptive value of the character cannot be identified, in many instances, those characters are still valid.

Many characters were initially included in this analysis. The following characters were excluded because of high variance between and within species: thickness of the lamina and midrib, thickness of first, second and third order vascular bundles, presence or absence of leaf ribs and furrows, type of midrib, type of first, second and third order vascular bundle sheath (complete or incomplete), number of cells forming the first, second and third order vacular bundle sheaths, number of stomata per surface unit, interstomatal cells shape, silica bodies shape, silica bodies ends, type of inflorescence, length of inflorescnece, spikelets length, type of callus, proportion awn/spikelet, and altitude.

The cladistic analysis was carried out following two different lines. First, a manual attempt was done. The steps followed in this analysis included: 1. Selection of a presumed monophyletic group. 2. Selection of an outgroup. 3. Selection of characters. 4. Determination of character-states (polarization). 5. Grouping of taxa by shared derived-characters. Second, by using the computer program PHYLIP (Phylogeny Inference Package, version 2.8). Within this package, the programs that were run were those usable for analyzing discrete data. MIX (Wagner, Camin-Sokal, and mixed parsimony methods), DOLLOP (Dollo and polymorphism parsimony methods), CLIQUE (Compatibility methods), BOOTM (Bootstrap confidence interval on the above parsimony methods), and BOOTDOL (Bootstrap confidence on Dollo, polymorphism parsimony).

1. Phylogeny of the genus Sorghastrum

The genus Sorghastrum has been associated taxonomically with several different genera. Based on this fact, one of the main objectives of this investigation is to locate the genus Sorghastrum as a real and identifiable taxon, within a phylogenetic frame.

I consider the Andropogoneae as a monophyletic group, sharing a common ancestor shown by the synapomorphies "single bundle sheath", "Kranz-MS photosynthesis" and "spikelets arranged in rames".

With respect to the selection of the outgroup, which is often considered as one of the most critical problems in cladistics (Duncan and Stuessey, 1984), the genus Saccharum was chosen. This genus is considered primitive within the subtribe Saccharinae, which probably is the most primitive subtribe of Andropogoneae (Clayton and Renvoize, 1986). Even though it is recognized that Saccharum is not plesiomorphic (=primitive) in all the respects, it provides a good comparison and starting point for a further polarization of characters.

The remainding genera included in this phylogenetic analysis were selectively chosen based on their apparent relationship with Sorghastrum, as well as the taxonomic information available for each genus. The optimal phylogenetic analysis should be the comparison of all Andropogoneae genera. However, the lack of systematic information for many taxa hinders it.

The characters and character-states considered in this cladistic

analysis are the following:

1. Short cells paired vs. short cells solitary.

2. Midrib formed by few-many vascular bundles vs. midrib (at least in some species) formed by one vascular bundle.

3. Chlorenchyma inconspicuously or incompletely radiate vs. chlorenchyma completely radiate.

4. Long cells rectangular vs. long cells square.

5. Obscure inner bundle sheath present, in addition to a well developed bundle sheath vs. a single bundle sheath present, never with an inner sheath.

6. Sessile and pedicelled spikelets alike vs. sessile and pedicelled spikelets different.

7. Reduced pedicelled spikelet vs. suppressed pedicelled spikelet.

8. Pedicelled spikelet suppressed, but the pedicel present vs. both pedicelled spikelet and pedicel suppressed.

9. Rames paniculate vs. other type of rame arrangement.

10. Rames not arranged in panicles, forming rames racemose vs. rames forming rames digitate.

11. Rames without spatheoles vs. Rames with spatheoles.

The following matrix was obtained, based on the polarization of the characters. Number "0" represents a primitive state for this specific character, whereas number "1" expresses an advanced state for a certain character.

Table 2. Distribution of character-states in some selected Andropogoneae genera

TAXA	CHARACTER										
	1	2	3	4	5	6	7	8	9	10	11
Outgroup	0	0	0	0	0	0	0	0	0	0	0
Sorghum	0	0	1	0	1	1	0	0	0	0	0
Sorghastrum	1	1	1	0	1	1	1	0	0	0	0
Cleistachne	1	0	1	0	1	1	1	1	0	0	0
Dichanthium	0	0	1	1	1	0	0	0	1	1	0
Bothriochloa	0	0	1	0	1	0	0	0	0	0	0
Andropogon	0	0	1	0	1	0	0	0	1	0	1

In relation to the character-states "short cells paired" and "short cells solitary" (character 1), the polarity was determined by reference to the outgroup. I consider the character-state "short cells paired" as a primitive state. Consequently, the character-state "short cells solitary" is considered advanced. This synapomorphy is shared by Sorghastrum and Cleistachne.

With respect to character No. 2, it is generally observed that the midrib in Panicoid leaves usually has many vascular bundles. For this reason, the primitive character-state considered for this series is "midrib formed by many vascular bundles", whereas the advanced character-state is "midrib formed by a single vascular bundle". The latter is the case of some species of Sorghastrum.

The radiate arrangement of chlorenchyma cells in the leaf mesophyll of Kranz species is generally considered advanced (character 3). Meanwhile an inconspicuous or incomplete radiate chlorenchyma should be considered primitive. The synapomorphy (radiate chlorenchyma) is shared by all taxa except the outgroup.

The character-states related with the shape of the intercostal long cells (character 4), were determined by reference to the outgroup. The character-state "long cells rectangular" is a plesiomorphy (primitive state) shared by all taxa except Dichanthium.

In relation to the vascular bundle sheath of Kranz species (character 5), it is assumed in this work that a single bundle sheath is an advanced state. On the other hand the presence of two bundle sheaths is considered primitive. The advanced character state is shared by all the taxa except the outgroup.

With respect to the external morphology, the common evolutionary tendency of the spikelets in Andropogoneae, is the reduction of the pedicelled spikelets (character 6). The character state "sessile and pedicelled spikelets alike", is determined as primitive. It is shared by Saccharum (outgroup), Dichanthium, Bothriochloa, and Andropogon. The advanced character-state is considered "sessile and pedicelled spikelets different". It is shared by Sorghum, Sorghastrum and Cleistachne.

Within those taxa where spikelets are different, a general evolutionary tendency from reduction to suppression of the pedicelled spikelet occurs (character 7). The character-state "pedicelled spikelets

reduced" is considered primitive. Meanwhile the character-state "pedicelled spikelet suppressed" is advanced. Sorghastrum and Cleistachne share this synapomorphy.

Between Sorghastrum and Cleistachne (both with suppressed pedicelled spikelet), a primitive character-state is observed for the former, where the pedicel is still present (character 8). On the other hand, the advanced state for the character "presence or absence of the pedicel", is shown by Cleistachne where the pedicel is completely suppressed.

With respect to the evolution of the inflorescence between the taxa, it is well documented that Andropogoneae has an inflorescence unit called "Rame" (Pohl, 1980). It is accepted that the primitive stage of the inflorescence arrangement (character 9), is paniculate, whereas racemose or digitate arrangements are considered advanced states. The genera with non-paniculate rames are Dichanthium and Andropogon.

In relation to the evolution of the inflorescence, the genera that do not have paniculate rames may have racemose rames (character 10) or digitate rames. The character-state "rames racemose" is considered primitive, meanwhile "rames digitate" is considered advanced. This autoapomorphy is shown by Dichanthium.

Within those taxa that have rames paniculate, a secondary modification of some inflorescence branches might have permitted the origin of a protective and differentiated structure (spatheole) that covers and protects the inflorescence (character 11). This is considered an advanced character-state. Meanwhile, the absence of this spatheole is a primitive character-state. The genus that has this autoapomorphy is

Andropogon.

Two principal clades appeared in this cladogram (Fig. 32). The first clade includes the genera Sorghum, Sorghastrum and Cleistachne. These genera share the synapomorphy "sessile and pedicelled spikelets different" which is a recognized evolutionary tendency in Andropogoneae.

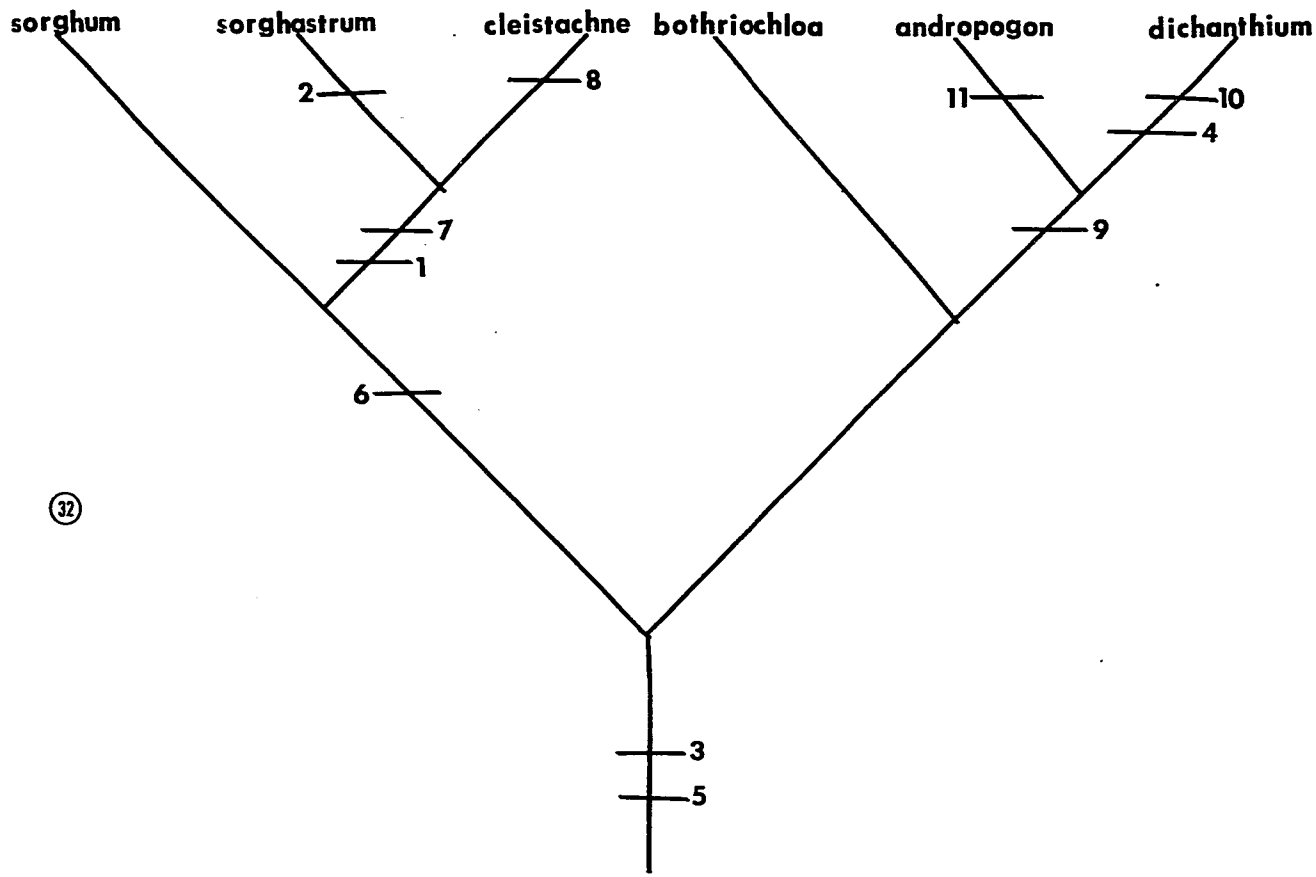
Sorghastrum and Cleistachne are sister groups, they share the most recent synapomorphies "presence of solitary short cells" and "pedicelled spikelet completely suppressed". The latter represents one of the major evolutionary steps in the reduction of the "paired unit" in the Andropogoneae.

Cleistachne shows the autoapomorphy "pedicel completely suppressed". With this genus, the end of a very well defined evolutinary tendency towards the reduction and suppression of the pedicelled spikelets in Andropogoneae is probably completed.

On the other hand, Sorghastrum shows the autoapomorphy "midrib, at least in some species, formed by one vascular bundle". Since the Panicoideae generally have a compound midrib (Metcalfe, 1960), this advanced character-state represents a very important stage. I suggest that this reduction in number and complexity of vascular tissue represents a recent evolutive state in the Andropogoneae towards the adaptation to drier zones.

The second clade is represented by the genera Dichanthium and Andropogon. Based on this analysis, these two genera represent a monophyletic group sharing the synampomorphy "rames not paniculate".

Figure 32. Cladogram of some selected genera of Andropogoneae. Single slash=apomorphy, double slash=homoplasy


sorghum
sorghastrum
cleistachne
bothriochloa
andropogon
dichanthium
2
8
11
10
4
7
9
1
6
3
5

(32)

Clayton and Renvoize (1986) affirm that terminal panicles occur in some of the more primitive genera in the Andropogoneae and that there is a strong tendency to reduction of the inflorescence. This inflorescnece reduction is apparent in Dichanthium and Andropogon neither of them showing paniculate rames. Furthermore, Dichanthium shows the autoapomorphy "rames digitate", which represents another tendency in Andropogoneae coupled to the former one, in which a multiplication in the number of inflorescences by repeated axillary branching is shown (Clayton and Renvoize, 1986). In addition, Dichanthium shows the autoapomorphy "long cells square". The polarization of this character was carried out by reference to the outgroup. Consequently, no further evolutionary interpretation can be done. Andropogon shows the autoapomorphy "rames covered by an spatheole". The assumption here, is that the spatheole represents an external and secondary protection to the reproductive elements of the plants.

On the other hand, based on the available data there is not any key to recognize a direct and recent phylogenetic association between Bothriochloa and the remainding genera. Therefore, there is little basis to place it on either of the remainding clades.

Sorghastrum represents a well defined genus, closely related to Sorghum and Cleistachne. As is shown in the cladogram, Sorghum probably represents part of the ancestral genomic stock from which Sorghastrum originated. On the other hand, Cleistachne represents a more advanced taxonomic entity than Sorghastrum, but probably directly originating from it.

There is not any reason for considering Bothriochloa a taxon originated from an evolutionary line diverging from a Dichanthium stock. The phylogenetic cladogram obtained shows that Dichanthium and Andropogon are more closely related among them, than with Bothriochloa. Probably an Andropogon-like stock, with racemose rames, gave rise to Dichanthium that has digitate rames. On the other hand, Bothriochloa probably represents the result of another evolutionary line parallel to Dichanthium. During the selection and polarization of characters, those that were more "useful", phylogenetically speaking, for carrying out this cladistic analysis were the anatomical characters. Considering that it has been recognized for many years, that the delimitations of the genera in the Andropogoneae has not been clear, the addition of these new anatomical data should be helpful for the delimitation of at least some genera.

It is important to point out that the phylogenetic relationships suggested in this work are the result of some morphological characters systematically studied in this dissertation. As more information of various sources is available, the cladogram and therefore the relationships suggested here within these genera may change.

2. Phylogeny of the species of the genus Sorghastrum

From the prior phylogenetic analysis of the genus Sorghastrum and some related genera, the probable phylogeny of the species of Sorghastrum represents the next logical step. This phylogenetic analysis is based on data accumulated by gross morphology studies, anatomical studies (leaf

cross sections, epidermal features observed in light microscopy, as well as using scanning electron microscope), ecology, distribution patterns, and phenology.

This analysis represents the first attempt to organize all the species of the genus Sorghastrum within a phylogenetic frame. The characters chosen, as well as their polarization, are based on assumptions taken from what is known within the Gramineae, the Andropogoneae, and especially using as much as possible the information systematically obtained in this work.

Because assumptions are carried out every time a polarization of a character takes place, the resultant cladogram may or may not represent a real phylogenetic trend for the species of the genus Sorghastrum. However, based on the available data, the following cladogram is the most parsimonious obtained (Fig. 33).

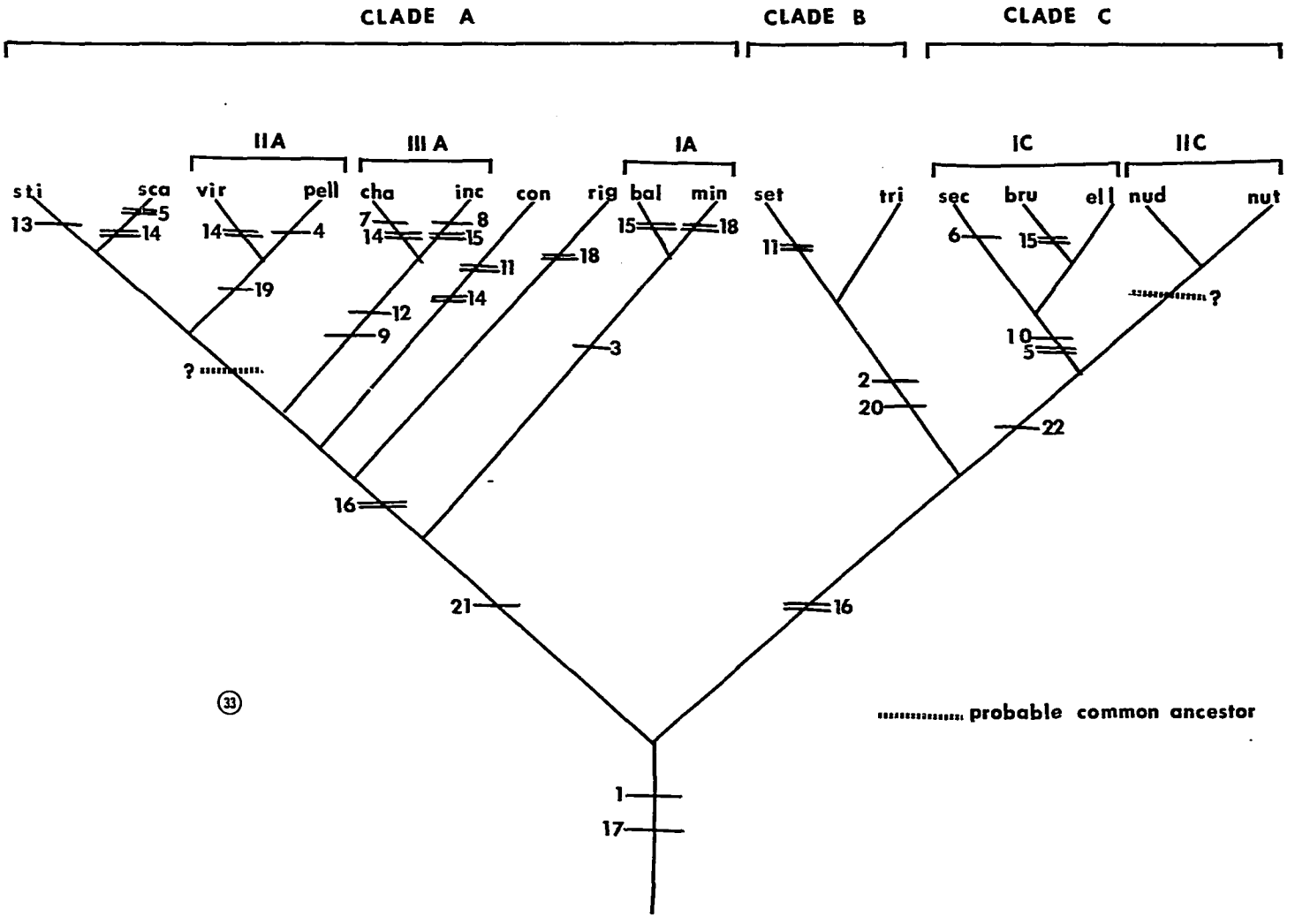
With respect to the selection of the outgroup, the genus Sorghum was chosen. This decision is based on the close relationship with Sorghastrum, and because it probably represents the main stock of the subtribe Sorghinae or the equivalent taxonomic rank (Clayton and Renvoize, 1986, Hartley 1958, and Keng 1939), to which Sorghastrum belongs.

The characters and character-states considered in this cladistic analysis are the following:

1. Pedicelled spikelet not suppressed vs. pedicelled spikelet suppressed.

2. Awn geniculate vs. awn straight.

Figure 33. Cladogram of Sorghastrum species. Single slash=apomorphy, double slash=homoplasy


CLADE A
CLADE B
CLADE C
IIA
III A
IA
IC
IIC
sti
sca
vir
pell
cha
inc
con
rig
bal
min
set
tri
sec
bru
ell
nud
nut
13
5
14
14
4
7
8
14
15
11
18
15
18
11
6
15
19
12
14
9
3
2
10
5
20
22
16
21
16
1
17
probable common ancestor

3. Awn length up to 6 cm long vs. awn length more than 6 cm long.

4. Second glume glabrous vs. second glume pubescent.

5. Spikelets pale vs. spikelets dark.

6. Inflorescence 2-sided vs. inflorescence 1-sided (secund).

7. Habit erect or nodding vs. clambering habit.

8. Plants perennial vs. plants annual.

9. Intercostal short cells angular vs. intercostal short cells rounded.

10. Angular intercostal short cells tall and narrow vs. angular intercostal short cells square.

11. Prickle hairs present vs. prickle hairs absent.

12. Prickle hairs all of one type vs. prickle hairs of two types.

13. Prickles with the base as long, shorter or slightly longer than the stomata vs. prickles with the base at least twice as long as the stomata.

14. Macrohairs absent vs. macrohairs present.

15. Costal zone formed by more than one file of cells vs. costal zone formed by one file of cells.

16. Stomata size in the abaxial size more than 3 um vs. stomata size in the abaxial size less than 3 um.

17. Silica bodies vertically elongated and situated in the intercostal zone present vs. silica bodies vertically elongated and situated in the intercostal zone absent.

18. Midrib compound vs. midrib simple.

19. Flowering period mainly in autumn vs. flowering period mainly in

spring.

20. Habitat terrestrial vs. habitat marshy or boggy.

21. Occurring in temperate vegetation (pine-oak forest) vs. occuring in dry vegetation (savannas).

22. Occurring in the Southern Hemisphere vs. occurring in the Northern Hemisphere.

The characters chosen for this cladistic analysis are those that present more stability in its expression. This character stability is understood as the holding of certain character expression independently of environmental variations.

The matrix (Table 3) includes the character states shown for each character in every species.

Character no. 1, shows the primitive state "pedicelled spikelet not suppressed" and the advanced state "pedicelled spikelet suppressed". The synapomorphy is shared by all the species of Sorghastrum, whereas in Sorghum (outgroup), a plesiomorphic (=primitive state) condition is observed. This derived condition represents one of the two advanced states defining the monophyletic character of all the species involved in this study. Consequently, it also defines the real phylogenetic entity of Sorghastrum.

The shape of the awn (character no. 2), is also a very stable parameter that has a primitive state "awn geniculate" and an advanced state "awn straight". The latter is considered advanced based on the assumption that the taxa showing this state (S. setosum and S. trichopus)

Table 3. Distribution of character-states in the species of the genus Sorghastrum

TAXON	CHARACTER																					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
balansae	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0
brunneum	1	0	0	0	1	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0	1
chaseae	1	0	0	0	0	0	1	0	1	0	0	1	0	1	0	1	1	0	0	0	1	0
contrac.	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	0	0	0	1	0
elliottii	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	1
incompl.	1	0	0	0	0	0	0	1	1	0	0	1	0	0	1	1	1	0	0	0	1	0
minarum	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0
nudipes	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1
nutans	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1
pellitum	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0
rigidif.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0
scaber.	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	1	0
secundum	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	1
setosum	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	1	0	0
stipoides	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	1	0
trichopus	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0
viride	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	0	1	0

have gone through a gradual reduction of the awn. This reduction can be explained due to the fact that they are well adapted to live in marshy or boggy areas. In Andropogoneae the awn does not necessarily have a dispersal function and probably it is mainly a "drilling" structure that permits the adequate establishment of the seed in the ground. If that is the case, the function of the awn in these two genera is definitely

unimportant and consequently its adequate development has not been retained by natural selection.

In relation with the awn length (character no. 3), the primitive state is considered "awn length up to 6 cm long" and the advanced one "awn length more than 6 cm long". The latter is the synapomorphy shared by S. minarum and S balansae. The same assumption referred in the prior paragraph (the main function of the awn in Andropogoneae is as a "drill" burying the seed in the ground) supports the polarization of these states. This means that among the taxa that show a well developed and geniculate awn, those with longer and stouter awns will accomplish the "drilling" function better than those showing smaller awns.

The morphology of the spikelet in the different species of Sorghastrum shows no significant modifications. However, an exception is observed with respect to the pubescence of the glumes (character no. 4). In all Sorghastrum species except S. pellitum, the first glume is pubescent, whereas the second one is glabrous. S. pellitum shows the autoapomorphy "both glumes pubescent". I assume that this increment in pubescence, is due to a protective adaptation of this latter species towards very dry environments.

The character states "spikelets pale" and "spikelets dark", primitive and advanced states respectively (character no. 5), were polarized in reference to the outgroup. In Sorghum species and even in most of Sorghastrum species, pale spikelets are more common than those with darker spikelets. This synapomorphy is shared by S. elliottii, S. secundum, S. brunneum, and S. scaberrimum.

Even though the inflorescence in Andropogoneae has evolved in many ways, it is not generally secund (primitive state). However, in S. secundum the inflorescence shows a distinct secund inflorescence that in this work is assumed to be a derived condition (character no. 6).

The erect habit (character no. 7) is common in the outgroup, in most of Sorghastrum species, as well as in Andropogoneae. However, S. chaseae shows a clambering habit, which is unique in Sorghastrum, and exceptionally rare in the Andropogoneae. Based on these facts, I assume that the clambering habit represents an advanced state or autoapomorphy of S. chaseae.

In relation with life duration (character no. 8), perennial and annual species represent a primitive and advanced state respectively. In the outgroup, as well as in Sorghastrum, except S. incompletum, perennial species are common. However, S. incompletum represents the only annual species of Sorghastrum. Annuality is assumed to represent a derived state within Sorghastrum.

As was already mentioned, many epidermal features have been found to be particularily helpful in the cladistic analysis. In character no. 9, the character state "intercostal short cells angular" is considered primitive, whereas "intercostal short cells rounded" is suggested as an advanced state. These assumptions are based in reference to the outgroup. The synapomorphy is shared by S. incompletum and S. chaseae.

Related to the former character, and again in reference to the outgroup, character no. 10 shows a primitive state "angular intercostal

short cells tall and narrow" and the advanced state "angular intercostal short cells square". This synapomorphy is shared by S. brunneum, S. elliottii, and S. secundum.

Prickle hairs (character no. 11) are a common epidermal feature in Gramineae. The Andropogoneae, the outgroup and Sorghastrum usually show prickle hairs. However, S. contractum and S. setosum do not show prickles on both leaf surfaces. The absence of prickle hairs is suggested as a derived condition shared by these two species.

It is known that through the different groups of Gramineae there is a great variety of prickle forms (character no. 12). However, each or a few forms are specific to each taxon or a few taxa. The outgroup and Sorghastrum show, in general terms, one prickle hair form. However, S. chaseae and S. incompletum show two types of prickle hairs instead of the single one. The latter is considered a synapomorphy shared by these two species.

In relation to the last two characters mentioned above, and in reference to the outgroup, it is assumed that the prickle hair size (character no. 13) shows the primitive state "prickles with the base as long, shorter or slightly longer than the stomata". On the other hand, the advanced state is "prickles with the base at least twice as long as the stomata". This autoapomorphy is shown by S. stipoides.

The character states absence or presence of macrohairs (character no. 14) were polarized in reference to the outgroup. The absence of macrohairs represents a primitive state, whereas, its presence is assumed to represent an advanced condition. The synapomorphy is shared by S.

scaberrimum, S. chaseae, S. contractum, and S.viride. Even though the presence and absence of macrohairs has been associated with environmental changes, rather than to genetic ones, I assume that at least for Sorghastrum species the presence of macrohairs is a character state that is always expressed in the individuals of these four species, independently of the environmental conditions.

In reference to the outgroup, character no. 15 was polarized. The primitive state is considered "costal zone formed by more than one file of cells", meanwhile the advanced state is "costal zone formed by one file of cells." The synapomorphy is shared by S. balansae, S.brunneum, S. incompletum, and S. minarum.

The stomata are very important plant elements directly involved in CO_2 fixation, necessary for photosynthesis. This means that changes in their morphology or size within some taxonomic entities, may represent changes in the physiology of this specific plant group. The Andropogoneae are C_4 plants, with a typical and distinct NADP-ME anatomy (Ellis, 1977). This distinctive anatomy is closely related with the high efficency of these plants to fix and refix CO_2 even in drastic environmental conditions. Based on the above information, I assume that the character "stomata size" (character no. 16), can be polarized as follows: the primitive state is considered "stomata size more than 30 um", meanwhile the advanced state is "stomata size less than 30 um". Therefore the species showing the largest stomata are probably less efficent in Co_2 fixation than the ones with samller stomata. This

synapomorphy is shared by all the species except S. minarum and S. balansae.

In reference to the outgroup, the presence or absence of the silica bodies longitudinally elongated in the intercostal zone (character no. 17) was polarized. The primitive state is considered "silica bodies longitudinally elongated and situated in the intercostal zone". On the other hand, "silica bodies absent" is considered the advanced state. The synapomorphy is shared by all Sorghastrum species. This character state represents, along with character no. 1 (pedicelled spikelet suppressed) the derived condition joining in a monophyletic group all Sorghastrum species.

The midrib in Andropogoneae is generally compound (character no. 18). It is formed usually by several vascular bundle orders. Commonly it shows one first order vascular bundle and few-many second and third order vascular bundles. However, in S. minarum and S. rigidifolium a simple midrib formed by just one first order vascular bundle occurs. The latter is considered a synapomorphy shared by these two species.

In relation with their phenology (character no. 19) and habitat, some characters are worth pointing out. First, it has been discussed by Hartley (1958) that normally the Andropogoneae are adapted for flowering during the autumm. However, S. pellitum and S. viride mainly flower during the spring. This latter character state represents a derived condition.

With respect to the habitat (character no. 20), the Andropogoneae particularly inhabit savannas, and also extend into warm-temperate

regions. Because of this typical Andropogoneae habitat, I assume that the marshy or boggy habitat shown by S. setosum and S. trichopus represents an advanced state.

In relation to the prior character, the type of vegetation where the Andropogoneae presumably originated, was a temperate vegetation occurring in warm temperate regions of Asia (Hartley 1958). By means of the rapid and severe desertification of Africa, it seems possible that the Andropogoneae gradually invaded drier places. Based on this fact, I assume that habitat (character no. 21) has as a primitive state "temperate vegetation (pine-oak forest), whereas "dry vegetation" (savanna) corresponds to an advanced condition. The synapomorphy is shared by S. stipoides, S. scaberrimum, S. rigidifolium, S. viride, S. pellitum, S. chaseae, S. incompletum. S. contractum, S. balansae, and S. minarum.

Finally, the character "Hemisphere occurrence" (character no. 22), is directly involved with the prior one. Based on Hartley's hypothesis (1958), the probable origin of Andropogoneae was in the Southern Hemisphere. A further migration towards Northern regions took place later. The latter is considered a synapomorphy shared by S. brunneum, S. elliottii, S. secundum, S. nutans, and S. nudipes.

Three main clades are shown in the cladogram (Fig. 33). The first clade (clade A) consists of eight South American species, one occurring in South and Central America, as well as in Mexico, and one inhabiting Africa. All of them represent a monophyletic group by means of sharing

the synapomorphy "occurring in dry vegetation (savanna-type)". This clade, at the same time, is formed by three groups, as well as four single species without any derived condition clustering them.

The first group (IA) corresponds to Sorghastrum minarum and S. balansae, which appear as a monophyletic group sharing the synapomorphy "awn length more than 6 cm long". This group is excluded from the rest of Sorghastrum species due to the lack of the derived condition "stomata size in the abaxial surface less than 33 um". However, no autoapomorphy has been found for S. minarum and S. balansae.

Secondly, the next monophyletic group (II A) is formed by S. pellitum and S. viride. They share many morphological similarities, and I am very suspicious about a possible hybridization process taking place between them. They share the synapomorphy "flowering period in spring". S. pellitum shows the autoapomorphy "second glume pubescent".

Thirdly, a very interesting group (III A) is observed in this cladistic analysis. It is formed by S. chaseae and S. incompletum a species pair sharing the derived state "prickle hairs of two types" and "intercostal short cells rounded". These two species possess unique and distinctive characteristics within the genus. From the evolutionary point of view, S. chaseae is the only species in Sorghastrum that shows a clambering habit. On the other hand, S. incompletum is the only species in Sorghastrum that shows an annual cycle. In both cases their unique characteristics are assumed to represent their respective autoapomorphies.

Finally, S. stipoides, S. scaberrimum, S. rigidifolium, and S.

contractum represent the taxa that do not share any derived state. That means that with the information available no precise clustering can be made.

The second clade (clade B) is a very specialized and defined set. It is formed by S. setosum and S. trichopus which share the synapomorphy "awn straight" and "marshy or boggy habitat". I speculate that this clade represents a very advanced evolutionary line, successfully established in swampy or boggy places.

The third and last clade (clade C) is formed by five mainly North American species. It is defined as monophyletic by means of all the species sharing the synapomorphy "occurring in the Northern Hemisphere". This clade consists of two groups. The first group (IC), is formed by S. elliottii, S. brunneum and S. secundum. The last one shows a recent and different ancestor, due to the autoapomorphy "inflorescence secund"; whereas the two former do not show any derived character defining each of them. Finally, the last group (II C) is formed by S. nutans and S. nudipes that very likely have a recent derived condition (unknown in this work), that makes them a well defined group, related but different from the rest of the North American species.

With all this information extracted from the most parsimonious tree found, the next working hypothesis is proposed:

S. minarum and S. balansae (clade no. IA) represent the taxa with the fewest shared derived characters. These taxa, therefore, are considered the most primitive within Sorghastrum. They are monophyletic

and probably one is derived from the other. It seems that S. minarum probably originated from a line of S. balansae.

Within the same clade, the species S. minarum from the Americas and S. rigidifolium from Africa, show the same homoplasic condition. I speculate that S. minarum probably represents the American species that is more related to the African ones, especially to S. rigidifolium, which represents the most primitive African species.

In addition, the American species S. chaseae and S. incompletum (S. incompletum var. bipennatum (III A) in Africa, is considered an introduced variety) are closely related. Based on the probable area of origin of the genus, S. chaseae probably represents a more primitive line than S. incompletum. From S. chaseae stock a diverging line probably emerged, giving rise to a successful annual species (S. incompletum) that invaded mainly Central America and Mexico.

On the other hand, two more groups within the first clade should be mentioned here. First is the one formed by S. viride and S. pellitum (II A), and second is the possible group (with the data available there is no evidence) consisting of S. stipoides and S. scaberrimum. These four species seem, in my opinion, more closely related to one another than to the rest of the species of the first clade. In the cladogram, a break line is shown indicating that with the available data there is no synapomorphy showing the monophily of these four species. However, I expect this monophyletic condition to exist.

The third clade is formed by the North American species. It is considered a more recent evolutionary group than the former ones.

However, with the available data it is not possible to define the linkage between South American and North American species. Based on distribution ranges and morphological comparisons, the line of S. stipoides seems the most plausible connection with the Northern Hemisphere.

One of the species possibly originating from the S. stipoides stock was the widespread and successful S. nutans (II C). The latter is distributed all around Mexico, United States (except in the Northwest corner), and Southern Canada. The cladogram obtained shows that S. nudipes is probably a new evolutionary line emerging from the main S. nutans stock.

On the other hand, the second group of the third clade represents a well defined monophyletic group sharing the synapomorphy "angular intercostal short cells square". This group is formed by S. elliottii, S. brunneum, and S. secundum (IC). The first two species are closer to each other than to S. secundum, which shows a very distinctive autoapomorphy "inflorescence secund". S. secundum mainly occurs in Florida, which is probably a recent origin. On the other hand, S. elliottii has a wider distribution range, of the Southeastern U.S.A. surrounding the Appalachian Mountains, but not in Florida. Finally, S. brunneum is located mainly on the East Coast of Mexico and the Northern regions of Central America. Possibly, a S. brunneum-like stock was the genetic source for the former origin of S. elliottii and S. secundum. It seems that S. elliottii originated from an evolutionary line recently diverged, whereas S. secundum comes from an evolutionary line that

emerged earlier.

All these species belonging to clade IC occur mainly in temperate vegetation types (Pine-Oak Forests). However, S. nutans and S. nudipes of clade II C (especially the former) are quite flexible in relation to the environmental conditions where they occur. S. nutans may be present from high altitude pine-oak forests to low and dry scrub-like vegetation, as well as in temperate prairies. This environmental flexibility is considered in this work as the fact supporting the hypothesis that S. nutans is the linkage with the South American genome stock, probably through S. stipoides. However, the morphological differences between these species, as represented by three autoapomorphies separating them, might indicate a less direct relationship between S. nutans and S. stipoides.

Finally, the second clade (clade B) is represented by S. setosum from the Americas and S. trichopus from Africa. The cladistic analysis shows that they are a monophyletic group by means of sharing the synapomorphies "awn straight" and "species occurring in marshy or boggy places". They represent the most advanced species in this analysis. However, it is not clear species could possibly be the ancestor of this clade. The distribution range may suggest an ancestor occurring in the eastern part of South America, or West Africa (before the break-up of Gondwanaland). Even though S. setosum and S. trichopus are very advanced, the evolutionary line from which they emerged probably diverged from the ancestor a long time ago. This can explain the lack of a living representative of the ancestral line of these species.

Summarizing the results of the phylogenetic analysis, the following conclusions should be pointed out.

1. The most primitive species of Sorghastrum are S. minarum and S. balansae.

2. The most advanced species of Sorghastrum are S. setosum and S. trichopus.

3. S. contractum and S. rigidfolium are closer to S. balansae and S. minarum than to the rest of the South America species.

4. Probably a different evolutionary line in Sorghastrum is represented by S. incompletum and S. chaseae. It seems that these species have attempted different strategies than the remainder. S. incompletum is the only annual species, whereas S. chaseae shows a unique clambering habitat.

5. S. stipoides, S. scaberrimum, S. viride, S. pellitum, S. incompletum, and S. chaseae are well adapted to dry places.

6. Probably a S. stipoides-like ancestor has given rise in North America to the the third clade, formed by the North American species.

7. S. nutans and S. nudipes are flexible in their habit requirements and either can live in dry or temperate areas. On the other hand, S. secundum, S. brunneum, and S. elliottii are well adapted to temperate zones.

C. Evolution and Biogeography

Sorghastrum comprises 17 species located in either Africa or the Americas (Fig. 34). Eight are strictly South American (S. minarum, S. balansae, S. contractum, S. chaseae, S. pellitum, S. viride, S. scaberrimum, and S. stipoides). Two species are strictly African (S. rigidifolium and S. trichopus). Two species are distributed in Mexico, as well as Central America and South America (S. incompletum and S. setosum). One occurs in Mexico and Central America (S. brunneum).

Finally, four species are strictly North American (S. elliottii, S. secundum, S. nudipes, and S. nutans).

A reasonable explanation of the migration routes and the present distribution patterns of each species is not now possible. However, based on the phylogenetic analysis, as well as the present and the possible past distribution patterns of the taxa, some speculations might be attempted.

First, Sorghastrum probably originated from a Sorghum-like stock, in the present Eastern South America and/or Western Africa. This assumption is based on the phylogenetic analysis results. The analysis shows that the primitive South American species S. minarum and S. balansae are closely related to S. rigidifolium from Africa.

Second, further migration and subsequent radiation of Sorghastrum in South America resulted in new South American species. As is seen in the phylogenetic cladogram ,the species S. stipoides, S. scaberrimum, S. viride, S. pellitum, and S. contractum are closely related. Furthermore,

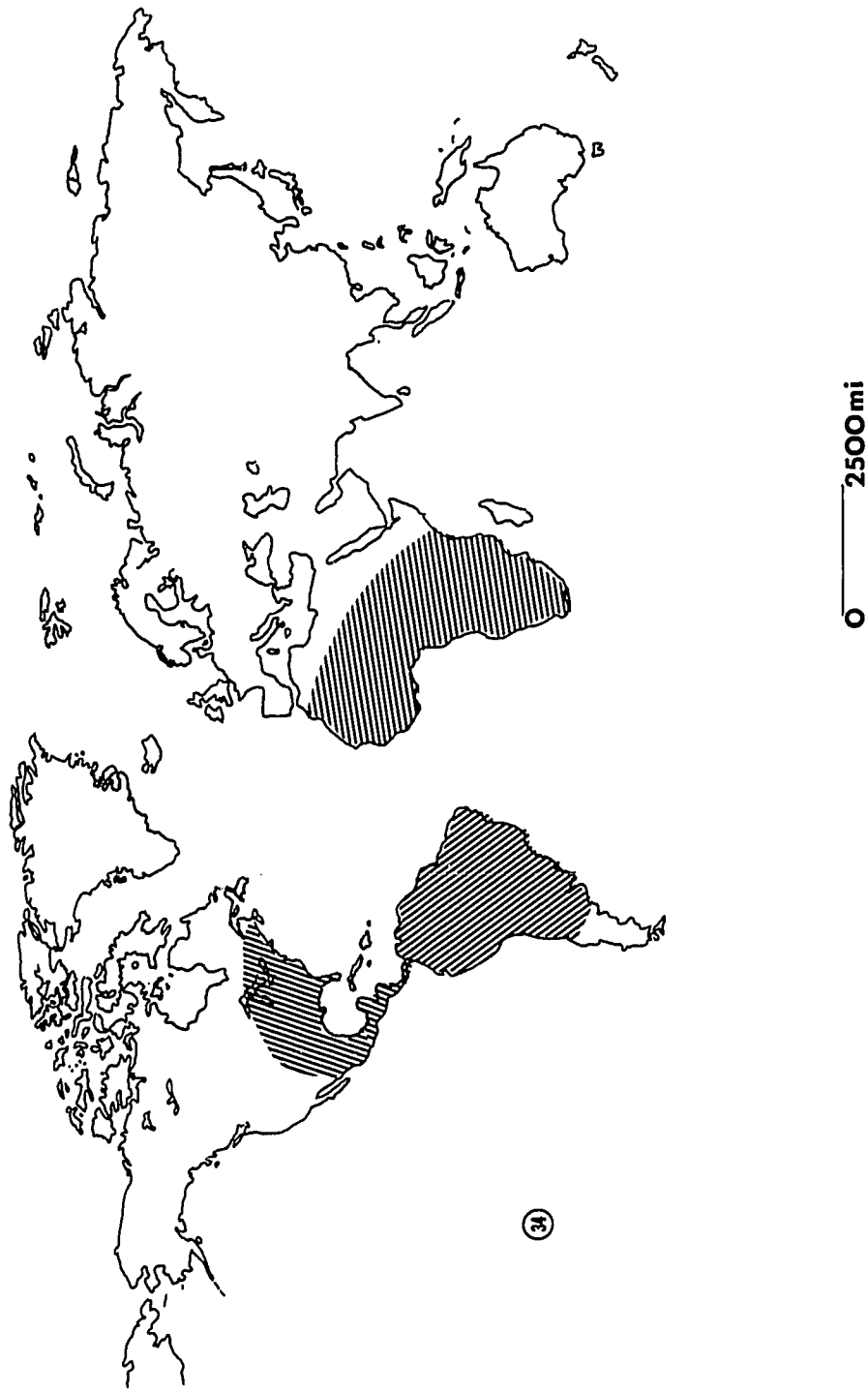
these species also show, in many cases, overlapping distribution ranges. This means probably that the zone inhabited by these species represents an ancient center of dispersion of Sorghastrum.

Third, some other species that are closely related show disjunct distribution patterns. S. setosum, a widespread species of the Americas, is phylogenetically close to the African species S. trichopus. On the other hand, S. chaseae from South America, is related to S. incompletum mainly inhabiting Central America and Mexico.

Fourth, probably a more recent group of species is the North American ones. As is indicated in the cladistic analysis, there is no available data showing any linking species among South American and North American species. However, it is assumed that an S. stipoides-like stock might have been the ancestral stock of the North American species.

Migration, long-distance dispersal or even land-mass movements may be involved in the explanation of this disjunct distribution. However, the lack of fossil record, as well as the lack of comparative information of other related taxa, make it impossible to explain the present distribution of Sorghastrum species.

Figure 34. Distribution of the genus Sorghastrum in the world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IX. TAXONOMIC DESCRIPTIONS

A. Sorghastrum Nash

Chrysopogon Trinius. Fund. Agrost. 187. 1820.

Poranthera Rafinesque, Bull. Bot. Geneve 1:221. 1830.

Chrysopogon sect. stipoides Bentham, Journ. Linn. Soc. 19:73. 1881.

Andropogon sect. Sorghastrum Fournier, Pl. Mex. 2:55. 1881.

Sorghum sect. Chrysopogon Hackel, Fl. Bras. 2(3):273. 1883

Andropogon subgenus Sorghum Hackel, DC. Monogr. Phan. 6:528. 1889.

Chalcoelytrum Lunell, Am. Midland Nat. 4:412. 1915.

Sorghum sect. Sorghastrum (Fournier) Stapf, Fl. Trop. Afr. 9:111. 1919.

Andropogon subgenus Sorghastrum (Fournier) Garber, Cyto. Stud. Gen. Sorghum. 283. 1950.

Sorghastrum Nash, Man. Fl. North U.S. 71. 1901. Holotype: Andropogon nutans L.

Diagnosis: Culms hollow, smooth and glabrous; leaves with serrulate margins; ligule membranous; inflorescence a terminal, compound, ebracteate panicle, with the primary branches ususally solitary, or in pairs and branched from the base appearing as if whorled, the real unit of the inflorescence is a rame, i.e., an unbranched axis that bears both sessile and pedicellate spikelets; spikelets paired, a pedicellate spikelet rudimentary with a pubescent pedicel present and the spikelet completely reduced, or rarely having 2 minute bracts; the sessile

spikelet dorsally compressed, with two indurate and subequal glumes; florets 2, the sterile floret represented only by a hyaline lemma; the fertile floret formed by lemma, palea (when present), and reproductive parts; the fertile lemma hyaline, ciliate, bifid, awned; the awn usually well developed, sometimes minute; lodicules 2, glabrous; stamens 3; ovary glabrous, styles distinct, stigmas plumose; fruit a caryopsis.

Description: Rhizomes well developed or lacking. Culms simple, caespitose, erect, nodding or, clambering (S. chaseae), from less than 50 cm to over 3 m tall. Internodes terete, smooth or sometimes slightly sulcate above the nodes, yellow, waxy, glabrous, except for the pubescence close to the nodes, or uniformly pubescent, hollowed. Nodes conspicuously pubescent, especially in young specimens. Leaves: blades expanded, inrolled or folded, pubescent on one or both surfaces, or glabrous; immature plants of the different species may show pubescent blades, margins serrulate; ligule membranous, glabrous or pubescent, truncate or forming long and well developed auricles (S. viride); sheath glabrous, or pubescent, longer or shorter than the internodes. Inflorescence a terminal panicle, dense (S. pellitum, S. minarum), loose (S. elliotti, S. incompletum) or semi-open, the inflorescence branches secund (S. secundum) or equilateral; erect or nodding, stout or fragile; branches bearing a few spikelets pairs; peduncles glabrous of hairy, capillary, often flexuous; rachis capillary, disarticulating at base of sessile spikelet, usually glabrous. Sessile spikelet dorsally compressed, lanceolate, oblong or linear-oblong, dark (S. brunneum, S.

scaberrimum), pale (S. stipoides, S. setosum, S. nutans, etc.) or yellowish (S. viride), bi-flowered, the lower floret reduced to a lemma, the upper floret perfect; callus blunt or pointed (very conspicuous in S. minarum), villous. Glumes 2, coriaceous, indurate, lanceolate; glume I acute, pubescent, 7-9-nerved; glume II truncate, slightly longer than glume I, usually glabrous and shining, sometimes pubescent (S. pellitum), 5-nerved. Sterile lemma hyaline, bifid, ciliate, 2-nerved, longer than the fertile lemma. Fertile lemma hyaline, ciliate, bifid, with an awn originating from the sinus, usually very reduced, 3-nerved. Palea hyaline when present. Awn straight and non-twisted (S. setosum) or once or twice geniculate and twisted, brownish and pubescent, usually from 1-3 cmm long, but sometimes along as 8 cm long (S. minarum). Stamens 3, filaments reduced, anthers well developed and occupying almost the whole floret cavity, oblong, yellowish or reddish. Lodicules 2, thin and glabrous. Ovary thin, glabrous. Caryopsis ellipsoid to obovoid, flattened.

Key to the Species of Sorghastrum

1a. Habit clambering, plants usually more than 2.50 m tall.....
.....S. chaseae

1b. Habit erect, or decumbent, plants less than 2.50 m tall.....2

2a. Awns straight, or sometimes once-geniculate, not twisted, 1-14 mm long; inhabiting wet areas (generally marshes or bogs)
.....3

2b. Awns once or twice-geniculate, twisted, generally more than 15 mm long; inhabiting savannas, woodlands or even wet areas, but not marshes and bogs.....4

3a. Spikelets 3.5-5 mm long, callus blunt; American.....
.....S. setosum

3b. Spikelets 5-7 (-9) mm long, callus pointed; African.....
.....S. trichopus

4a. Awn more than 5 cm long, 8 or more times longer than the spikelet.....5

4b. Awn less than 5 cm long, less than 8 times longer than the spikelet.....6

5a. Inflorescence strict and erect, dense, 10-25 cm long; awns dark, 11 or more times longer than the spikelet.....S. minarum

5b. Inflorescence erect, semi-open, 10-40 cm long; awns pale, not more than 9 times longer than the spikelet.....S. balansae

6a. Inflorescence secund (1-sided).....S. secundum

6b. Inflorescence equilateral.....7

7a. Glume II pubescent, inflorescence conspicuously villous.....
.....S. pellitum

7b. Glume II not pubescent, the inflorescence not conspicuously villous
.....8

8a. Culms decumbent, rooting at the lower nodes; inflorescence loose; annual plants.....9

8b. Culms erect or slightly nodding, but not decumbent; inflorescence loose or dense; perennial plants.....10

9a. Awns 10-35 mm long, 4-6 times longer than the spikelets; culms about 1 m tall.....*S. incompletum* var. *incompletum*

9b. Awns 35-45 mm long, 7-9 times longer than the spikelets; culms about 1.70-2 m tall.....*S. incompletum* var. *bipennatum*

10a. Spikelets deep chestnut-brown or black.....11

10b. Spikelets not deep chestnut-brown, pale.....12

11a. Spikelets 3.8-5 mm long; South American.....*S. scaberrimum*

11b. Spikelets more than 5 mm long; North and Central American.....13

12a. Leaves with very conspicuous auricles, usually 5-7 mm long.....14

12b. Leaves lacking obvious auricles, less than 3 mm long.....15

13a. Awn 25-40 mm long, 5 times longer than the spikelet; spikelets 6-7.5 mm long.....*S. elliottii*

13b. Awn 15-25 mm long, 3.5 times longer than the spikelet; spikelets 5-6.5 mm long.....*S. brunneum*

14a. Rhizomes present; inflorescence erect, brownish; North American.....*S. nutans*

14b. Rhizomes lacking; inflorescence erect or somewhat nodding, yellowish; South American.....*S. viride*

15a. Inflorescence loose, open; awns generally once-geniculate.....16

15b. Inflorescence not loose, linear-oblong; awns generally twice-geniculate.....17

16a. Branches and sub-branches of the inflorescence naked below the middle, with a few spikelets borne at the end; rhizomes present; spikelets 5.5-8.5 mm long; Mexico.....S. nudipes

16b. Branches and sub-branches of the inflorescence not naked below the middle, with many spikelets along the branches; rhizomes absent; spikelets 4-5.5 mm long; South American.....S. stipoides

17a. Inflorescence branches pointing upwards; callus of the spikelets sharpened; South American.....S. contractum

17b. Inflorescence branches not pointing upwards; callus of the spikelets blunt; African.....S. rigidifolium

B. Sorghastrum Species

1. Sorghastrum balansae (Hackel) Davila. Comb. Nov. Sorghum balansae Hackel, Fl. Bras. 2(3):277. 1883. Type: PARAGUAY. Jan 1877, Balansa 209 a (Holotype: P?). Not seen. (Figs. 35A, 35B and 35C).

Andropogon balansae (Hackel) Hackel, DC. Monogr. Phan 6:535. 1889. Based on Sorghum balansae Hackel.

Rhizomes lacking. Culms erect, many adventitious roots originating at the lower nodes, 3-4 (-4.5) mm diam., 1-2 (-2.60) m tall. Internodes terete, smooth and glabrous. Leaves: flat, 15-45 cm long, 2-6 (-7) mm wide, glabrous, in young specimens sometimes pubescent on the abaxial surface, apex acute, margins serrulate; ligule 1-3.5 mm long; sheath 20-35 (-44) cm long, 3.0-5.5 (-8) mm wide, glabrous. Inflorescence a dense

to semi-open panicle, erect, with ascending branches, panicle 10-40 cm long; rachis terete, glabrous; peduncle 30-65 (-85) cm long, glabrous. Spikelets lanceolate, dorsally compressed, 6-7.8 mm long; callus acute, 1.5-2.7 mm long, villous. Glumes coriaceous; glume I truncate, 5.5-7.3 mm long, 1.1-1.4 mm wide, pubescent, 7-9-nerved; glume II acute, 6-7.5 (-7.8) mm long and 1.1-1.3 (-1.6) mm width, glabrous, 5-nerved. Sterile lemma hyaline, bifid, 4-6.5 (-7.5) mm long, 0.6-1.5 mm wide, ciliate, 2-nerved. Fertile lemma hyaline, bifid, 3-4.5 (-6) mm long and 0.5-1.2 mm wide, ciliate, 3-nerved. Awn twice geniculate, 5-7.5 (-8) cm long, about 9 times longer than the spikelet. Anthers 2-4 mm long. Caryopsis unknown. Sterile Pedicel 3-5 (-6) mm long, pubescent. Chromosome number unknown.

Specimens examined: BRAZIL. GOIAS: Rio Verde, 2 Apr 1930, Chase 11706 (US); Mun. Joteiz, Quezada, 2 Sep 1950, Macedo 2130 (US); MATO GROSSO: Aquidauna, 26 Feb 1930, Chase 11056 (US); between Rondonopolis and Sao Lourenco, 9 Apr 1930, Chase 11931, 11919 (US); 1 km E of Km 264, Xavantina-Cachimbo road, 12 Mar 1968, Philcox & Fereira 4520 (WIS); tres Lagoas, 4-5 Feb 1930, Chase 10736 (US); MINAS GERAES: Pilves, Ituitaba, 3 Feb 1950, Macedo 2103 (US); Uberlandia, s.d., Macedo 4297 (US). PARAGUAY. Lake Ypacaray, Jan 1913, Hassler 12480 (MO); Icaz, s.d. Jorgensen 4574 (MO); MISIONES: Santiago, Estancia La Soledad, 7 Feb 1955, Pedersen 3287 (US).

Sorghastrum balansae is distinguished by having large awns, a semi-open panicle, as well as by showing ascending inflorescence branches that

are not very close to each other. This species may be confused with Sorghastrum minarum. However, the latter shows generally longer awns, as well as a denser inflorescence.

Sorghastrum balansae is distributed in the lowlands of South America (Fig. 36). It occurs in the countries of Brazil and Paraguay. In Brazil, it is present in the Eastern regions. In Paraguay, it occurs mainly in the Southern parts of the country. In those regions, the dominant vegetation types are savannas and cerrados.

Sorghastrum balansae flowers principally from January to March which corresponds to the autumn season in the Southern Hemisphere. The altitudinal range for this species varies from sea level to 500 m.

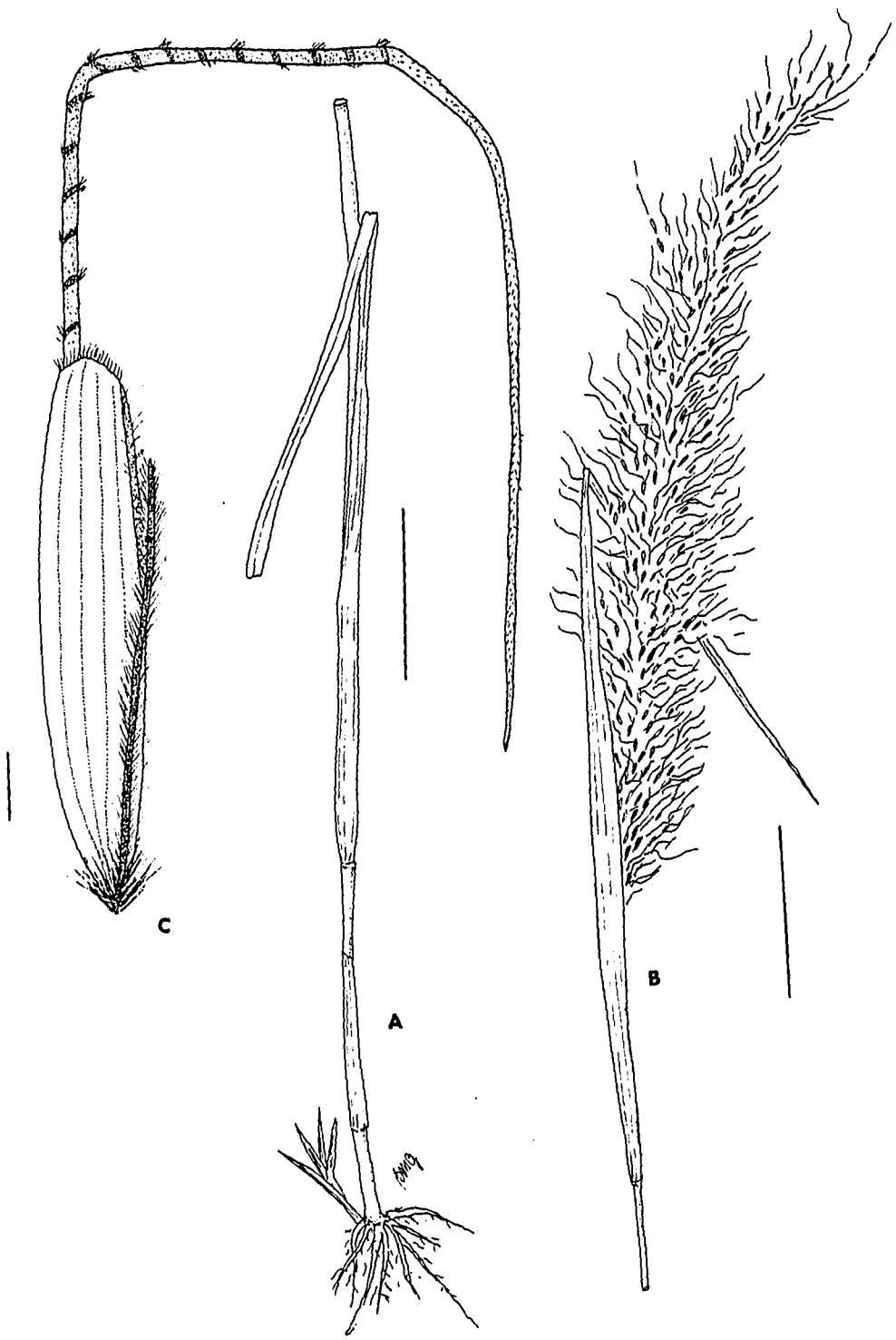
Sorghastrum balansae is probably related to Sorghastrum Minarum. Both species have morphological features in common and they are partially sympatric. S. balansae and S minarum grow in similar environmental conditions. However, the anatomical information supports the existence of two separate species.

NOMENCLATURE:

Hackel (1883) pointed out that in addition of the species Sorghum minarum there was a new species, similar to the former. He named this species Sorghum balansae. It is based in a specimen from Paraguay (Balansa 209a). The main difference cited by Hackel is that the present species shows a racemose panicle bearing many branchlets; instead of the panicle with few branchlets in S minarum.

In 1889, Hackel transferred all Sorghastrum species to the genus Andropogon. The author suggested the new combination Andropogon

Figure 35. Sorghastrum balansae. A. Basal part, bar=5 cm. B. Inflorescence, bar=5 cm. C. Ventral view of the spikelet, bar=1 mm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A
B

Figure 36. Distribution of Sorghastrum balansae


S. balansae
36
0
600 mi

balansae.

The legitimate name for the present species should be Sorghatrum balansae. Subsequently, the holotype specimen should be the one from Paraguay (Balansa 209a), which has not been located.

2. Sorghastrum brunneum Swallen, Contr. U.S. Natl. Herb. 29:428. 1949. Type: GUATEMALA. HUEHUETENANGO: in mountains W of Aguacatan, on road to Huehuetenango, 27 Dec 1940, Standley 81290 (Holotype: US!). (Figs. 37A, 37B and 37C).

Rhizome lacking. Culms erect, caespitose, 1-3 (-4) mm diam., 0.50-1.60 m tall. Internodes terete, smooth and glabrous. Leaves: blades flat to folded, 15-35 cm long, 2-6 (-7.5) mm wide, acute, scabrous and rarely pubescent above, scabrous below, margins serrulate; ligule decurrent, 2-4 (-5) mm long, ciliate; sheaths 14-30 (-40) cm long, (1.5-) 2-4.5 mm wide, generally glabrous, or pubescent at the margins in regions close to the ligule. Inflorescence an open panicle, erect or somewhat nodding, dark purple, 10-35 cm long; rachis terete, glabrous or scabrous; peduncle 15-55 cm long, glabrous. Spikelets dorsally compressed, lanceolate, deep chestnut brown at maturity, 5-6.5 mm long; callus 1-1.3 mm long, villous. Glumes obtuse, coriaceous; glume I truncate, 4.5-6 (-7.3) mm long, 1-2 mm wide, pubescent, 7-9-nerved; glume II acute, 5-6.5 mm long, 1-1.8 mm wide, glabrous, 5-nerved. Sterile lemma bifid, hyaline, 3-5 (-6) mm long, 0.5-1.5 mm wide, ciliate, 2-nerved. Fertile lemma bifid, hyaline, 2-5 (-6) mm long, 0.8-1.4 mm wide, 3-nerved. Awn well developed, twice-geniculate, 15-25 mm long, 3.5 times longer than the spikelet. Anthers brownish, 2-3.5 (-1.7) mm long. Caryopsis

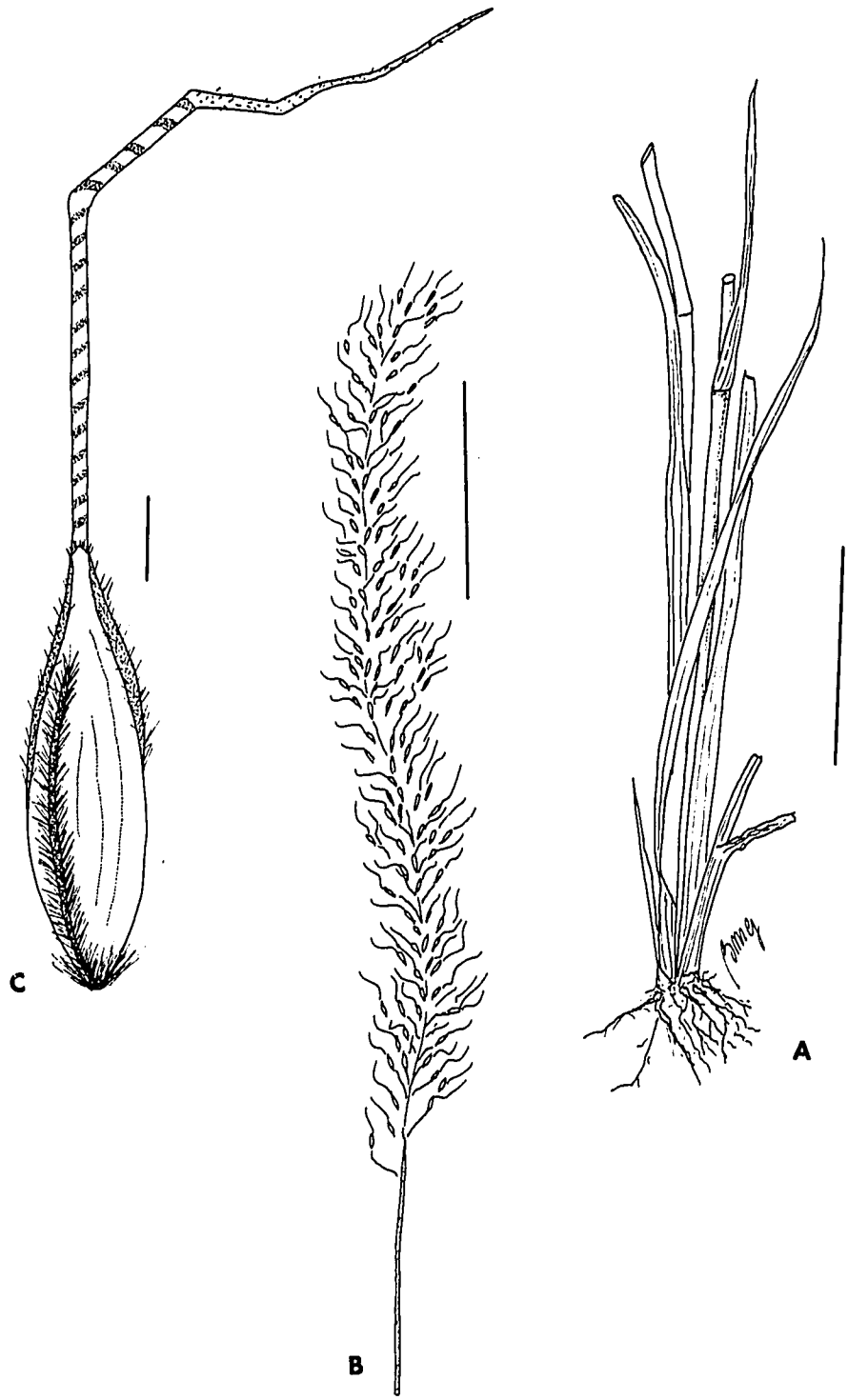
reddish, 2-2.5 mm long. Sterile pedicel 3.5 mm long. Chromosome number 2n=20.

Representative specimens examined: GUATEMALA. Guatemala city, 1-3 Dec 1911, Hitchcock 9132 (US); CHIQUIMULA: Montana Castilla, vicinity of Montana Cebollas, along Rio Lucia Saso, 3 miles SE of Quezaltepeque, 6 Nov 1939, Steyermark 31325 (F); GUATEMALA: on old road to San Lucas, vicinity of San Rafael, 27 Sep 972, Molina & Molina 27628 (ENCB, F, MO); HUEHUETENANGO: La Sierra (Tujimack), across river from San Lucas Atitan, Sierra de los Cuchumatanes, 8 Sep 1942, Steyermark 51983 (F, US). HONDURAS. COMAYAGUA: vicinity of Siguatepeque, 14-27 Feb 1928, Standley 56224 (US); MORAZAN: 2.5 km N of Zamorano on road to San Francisco de Soroguara, 1 Jul 1970, Pohl & Davidse 12139 (ISC). MEXICO. CHIAPAS: 15 km SE os San Cristobal, 22 Oct 1973, Gould & Hatch 14412 (ISC, MO, TEX); 15 miles SE of Teopisca in area of pines, oaks and junipers, 21 Aug 1953, Reeder & Reeder 2037 (ENCB); Mun. Tenejapa, along the river of Chik Ha' barrio of Yashanal, paraje Matsab, 17 Jul 1965, Breedlove 1126 (US); Mun. Venustiano Carranza, 3 miles S of Aguacatenango, along road to Pinola Las Rosas, 13 Oct 1965, Breedlove & Raven 13123 (ENCB, LL, US); COAHUILA: Mun. Saltillo, Sierra Zapaliname, 1 km al S del canon de Jacala, 12 Nov 1970, Rzedowski 27684 (ENCB); Mun. Molango, vicinity of Molango on road to Lolotla, 9 Nov 1946, Moore 2004 (US); NUEVO LEON: Hacienda Pablillo, Galeana, 26 Aug 1936, Taylor 230 (F); OAXACA: near Reyes, 20 Oct 1894, Nelson 1807a (US); Las Sedas, Sep 1894, Smith 917 (MO); PUEBLA: Alta Luz, Sep 1907, Purpus 2897 (F, NY, US); QUERETARO: 16 miles E of Landa

on the winding mountain road toward Xilitla, 12 Dec 1960, Johnston 6114 (TEX); SAN LUIS POTOSI: 8 km al SO de Guadalcazar, 10 Nov 1955, Rzedowski 6813 (ENCB); 34 miles of San Luis Potosi, on the Rio Verde Hwy., 6 Nov 1960, Johnston 6024 (LL, TEX, US); Mun. Cerritos, Ejido San Isidro, 3 Nov 1980, Bravo 43 (COT); Mun. Zaragoza, Sierra de Alvarez, cerca de Huerta, 3 Sep 1954, Rzedowski 4065 (ENCB); TAMAULIPAS: Mun. Gonzalez, Cardiel, Oct 1977, Villegas 269 (COT); Mun. Jaumave, 8 Sep 1981, Barrientos 67 (COT); Mun. Villa de Casas, central part of the Sierra de Tamaulipas, on the road from Rancho Las Yucas to Santa Maria de los Nogales and Hac. Acuna, from Cerro de San Juan to Santa Maria de los Nogales, 22 Sep 1956, Martinez & Borja F-2042 (TEX, US); VERACRUZ: Cumbres de Acultzingo, near top of ridge overlooking valley, 4 km SW of Acultzingo on Hwy. 150, at Km 283, 17 Aug 1965, Roe et al. 1273 (ENCB); Mun. de Jilotepec, Equilon, 6 Nov 1971, Ventura 4465 (ENCB); NO de Orizaba, 14 Dec 1959, Rzedowski 121159 (ENCB); Totutla, Oct 1841, Liebmann s.n. (US); Totutla, s.d., Liebmann 5950 (C).

Sorghastrum brunneum is distinguished from S. elliottii by its smaller spikelets and shorter awns. The awns in S. brunneum are 3.5 times longer than the spikelet, whereas in S. elliottii they are 5 times longer than the spikelet. S. brunneum occurs in Mexico and Central America. Sorghastrum elliottii is present in the southeastern regions of the United States, surrounding the Appalachian Mountains. Sorghastrum brunneum grows at higher regions than Sorghastrum elliottii. Also, S. brunneum grows generally in argillaceous soils, meanwhile S. elliottii is commonly found in sandy areas.

Figure 37. Sorghastrum brunneum. A. Basal part, bar=5 cm. B. Inflorescence, bar=5 cm. C. Ventral view of the spikelet, bar=1 mm .pa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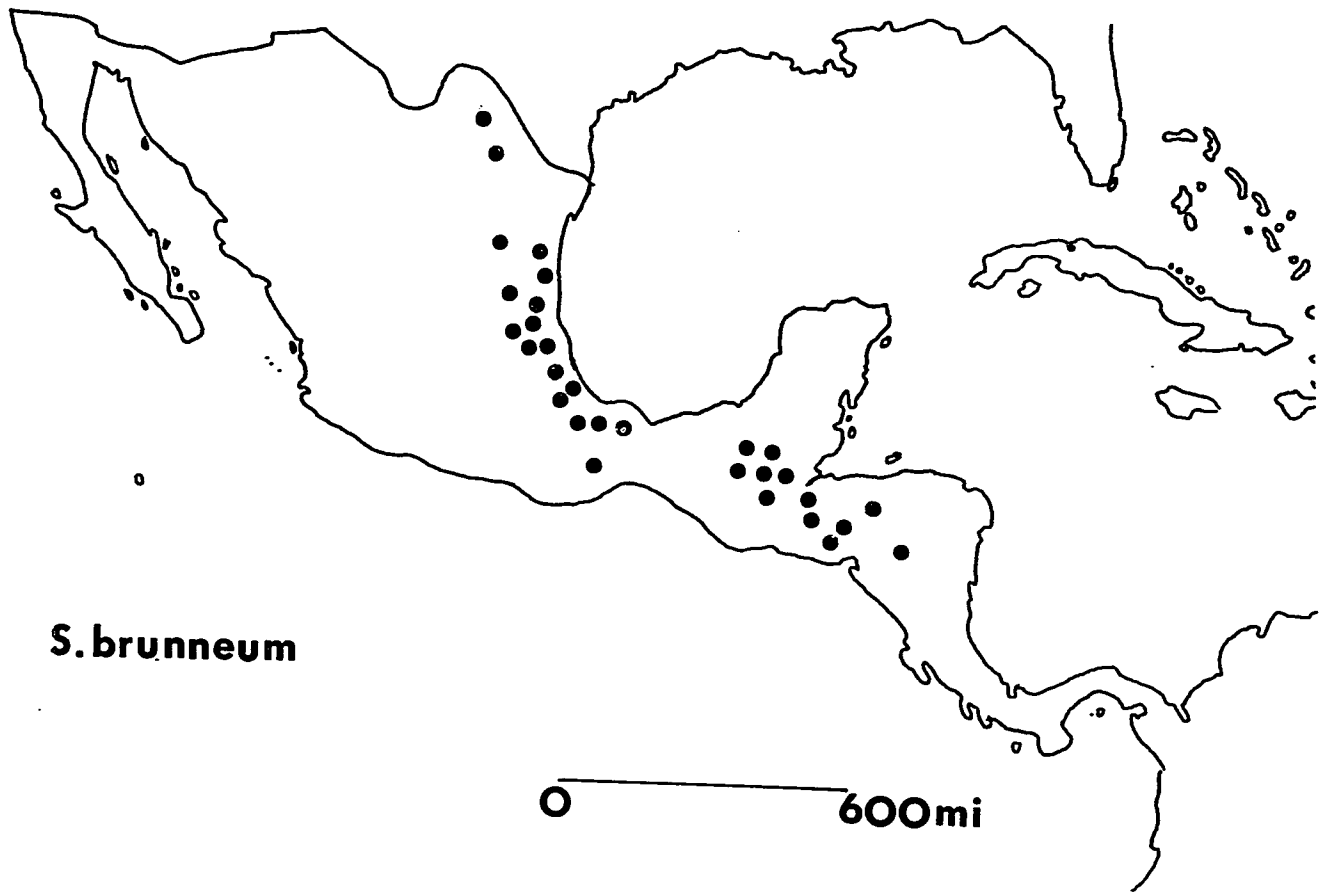
B
A

Figure 38. Distribution of Sorghastrum brunneum



(38)

Sorghastrum brunneum occurs in the Eastern regions of Mexico, from Tamaulipas to Veracruz and Chiapas, along the Sierra Madre Oriental. S. brunneum is also located in Guatemala and Honduras (Fig. 38). It inhabits altitudes from 1200-3000 m.

Sorghastrum brunneum inhabits oak forests, grasslands, deciduous forests and scrub-like vegetation. It flowers mainly from August to November, in autumn. Sometimes some individuals of this species may flower in December or May.

Sorghastrum brunneum and Sorghastrum elliottii are closely related. The latter inhabits lowlands, dry woods and sandy soils, in southeastern United States. On the other hand, S. brunneum inhabits higher regions, pine-oak forests and usually argillaceous soils, in Mexico and Central America.

Sorghastrum elliottii has longer spikelets and awns, as well as an awn/spikelet ratio larger than S. brunneum. Also, Sorghastrum elliottii has globose papillae, whereas Sorghastrum brunneum has slightly curved papillae that overarch the stomata.

3. Sorghastrum chaseae Swallen, Phytologia 14(2):96. Type: BRAZIL. MATO GROSSO: Santa Rita do Araguaya, 5-6 Apr 1930, Chase 11861 (Holotype: US!). (Fig. 39).

Rhizomes lacking. Culms clambering, usually supported by other plants, with many adventitious roots originating at the lower nodes, 3.5 mm diam., 2.50-3 m tall, glabrous. Leaves blades flat, expanded, 25-50 cm long, 20-25 mm wide, finely scabrous in both surfaces, margins serrulate; ligule firm, indurate, 3-5 mm long; sheaths shorter than the

internodes, 8-10 cm long, 5-6 mm wide, glabrous. Inflorescence open, branches ascending 20-40 cm long, the tip of the branches and branchlets hispid; rachis hispid; peduncle 50-60 cm long, glabrous. Spikelets dorsally compressed, lanceolate, greenish, 4.5-5 mm long. Glumes coriaceous; glume I truncate, 4-4.5 mm long, 1-1.2 mm wide, strongly pubescent, 7-9-nerved; glume II acute, 4.5-5 mm long, 1-1.2 mm wide, glabrous, 5-nerved. Sterile lemma hyaline, bifid, 3-4 mm long, 0.9-1.2 mm wide, ciliate, 2-nerved. Fertile lemma hyaline, bifid, 2-3 mm long, 0.05-0.1 mm wide, ciliate, 3-nerved. Awn twice geniculate, 2.5-3.5 cm long, 5-6 times longer then the spikelet. Anthers 2-3 mm long. Caryopsis 3 mm long. Sterile Pedicel 3-3.5 mm long, pubescent. Chromosome number unknown.

Specimen examined: BRAZIL. GOIAS: Sta. Rita do Paranayba, 31 Mar 1930, Chase 11644 (US).

Sorghastrum chaseae is distinguished by its clambering habit, as well as by its elongated culms, larger than the rest of Sorghastrum species. It may be confused with Sorghastrum contractum because of the semi-open inflorescence, the length of the awns (about 3 cm) that are not as long as those of S. minarum and especially because these two species usually form adventitious roots that originate from the lower nodes of the culm.

Sorghastrum chaseae is distributed in South America, in Brazil, in the States of Goias and Mato Grosso (Fig. 40). It is probably well adapted to lowlands (about 500 m) and dry and sandy places. The type of

Figure 39. Sorghastrum chaseae. Ventral view of the spikelet, bar=1 mm

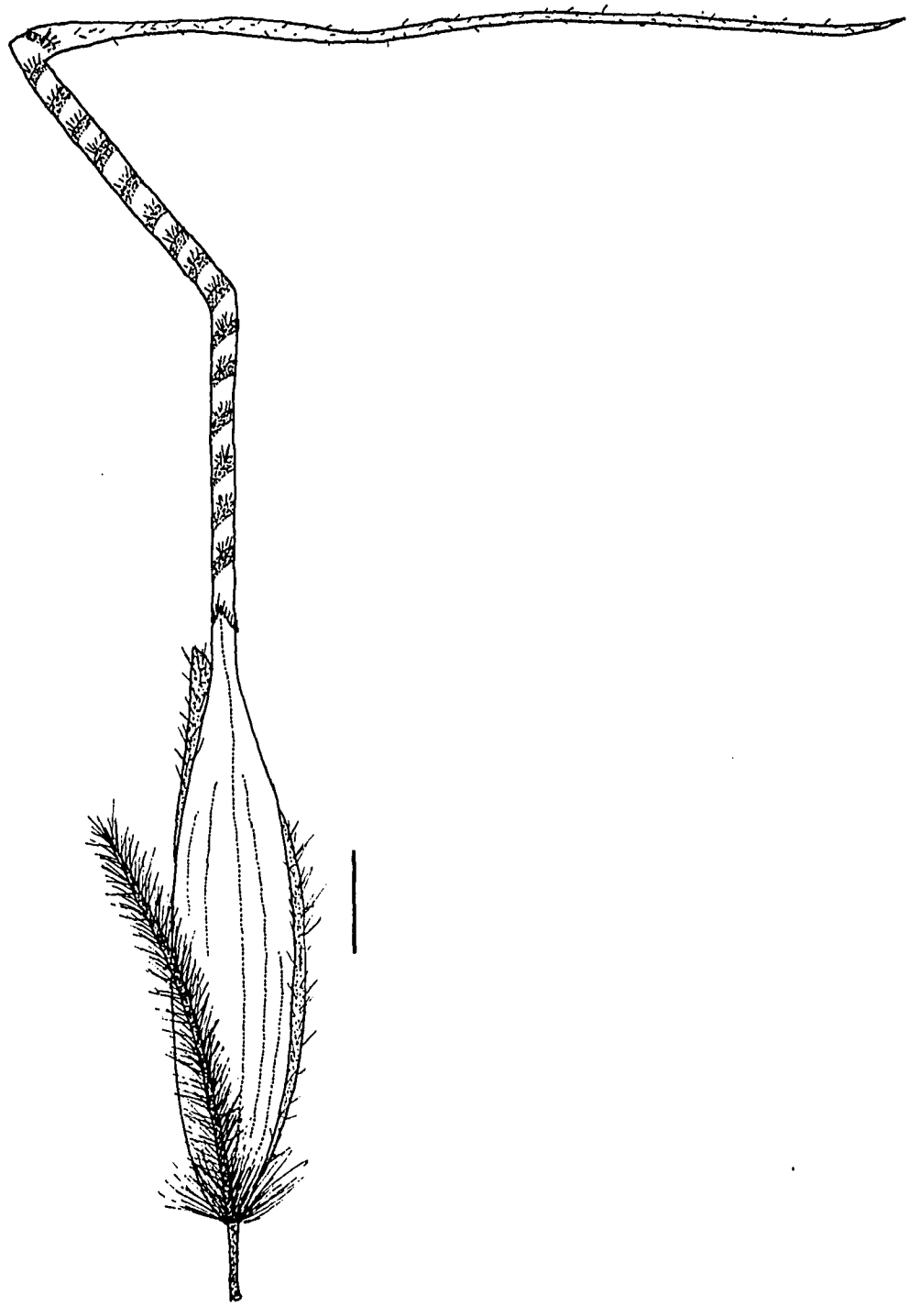


Figure 40. Distribution of Sorghastrum chaseae


S. chaseae
40
0
600 mi

vegetation dominating these areas is savannas or cerrados. It flowers from March to April, corresponding to the autumn in the Southern Hemisphere.

The principal limitation in considering this species is the lack of a representative number of specimens. Only two specimens were observed, the type specimen from Mato Grosso and a second one from Goyaz. However, in spite of the lack of representative specimens, the individuals observed show characters that differ from the other Sorghastrum species inhabiting the same or adjacent areas. The clambering habit that is observed, and that has been pointed out by Chase in both herbarium labels, is determinant in supporting the decision to accept S. chaseae as a legitimate species.

It is obvious that Sorghastrum chaseae needs further study. Collection of this species in areas close to those mentioned or with similar environmental conditions should be carried out. However, even though limited information is available it is better to support the legitimacy of this species, until further information will reject or agree this decision.

S. chaseae represents a species in which its unique clambering habit within the genus Sorghastrum possibly represents a further step towards its successful establishment in shrubby-type vegetation.

Even though it is morphologically similar to S. contractum, it seems that from the phylogenetic point of view, S. chaseae is related to S. incompletum. These two species posses unique and very distinctive characteristics within the genus. S. chaseae is the only species with

clambering habit. In addition, S. incompletum is the only annual species in the genus.

4. Sorghastrum contractum (Hackel) Kuhlmann & Kuhn, Fl. Dtto. Ibiti 29. 1947. Sorghum nutans Gray ssp. contractum Hackel, Mart. Fl. Bras. 2(3):276. 1883. Type: BRAZIL. Lagoa Santa, s.d., Warning s.n. (Lectotype: W!; Syntype: MO!). (Fig. 41A, 41B and 41C).

Andropogon nutans L. var. contractus (Hackel) Hackel, Dc. Monogr. Phan. 6:533. 1889. Based on Sorghum nutans ssp. contractum.

Sorghastrum amplum Swallen, Phytologia 14(2):95. 1966. Type: BRAZIL. SAO PAULO: on open hills, Sao Joao, 19 Mar 1922, Holway & Holway 1658 (Holotype: US!).

Rhizomes lacking. Culms erect, stout, caespitose, with many short extravaginal innovations, 2-4 mm diam., 1.20-2 (-2.30) m tall. Internodes terete, smooth and glabrous. Leaves: blades flat or convolute, 25-50 cm long, 2-8 mm wide, glabrous or slightly pubescent at the abaxial surface, sometimes scabrous, margins serrulate; ligule decurrent, 2-3.5 mm long, glabrous; sheaths 15-40 cm long, 2-5 mm wide, glabrous, sometimes pubescent close to the ligular areas. Inflorescence linear, dense, strict, sometimes loosely arranged, the inflorescence branches pointing upwards, 15-35 cm long; rachis terete, glabrous; peduncle (20-) 30-50 cm long, glabrous. Spikelets lanceolate, dorsally compressed, 4-6 mm long; callus sharpened, villous. Glumes coriaceous; glume I truncate, 4-5.5 mm long, 1-1.3 mm wide, pubescent, 7-9-nerved; glume II acute, 4.5-6 mm long, 1-1.3 mm wide, glabrous, 5-nerved.

Sterile lemma hyaline, bifid, 3.5-5 mm long, 0.7-1.2 mm wide, ciliate, 2-nerved. Fertile lemma hyaline, bifid, 2.6-4 mm long, 0.5-1 mm wide, ciliate, 3-nerved. Awn twice geniculate, twisted, 1.8-3.5 cm long, 4-5.5 times longer than the spikelet. Anthers 2-3 mm long. Caryopsis unknown. Sterile Pedicel 2.5-4 mm long, glabrous. Chromosome number unknown. Specimens examined: BRAZIL. MATO GROSSO: between Campo Grande and Dourados, 14-17 Feb 1930, Chase 10898 (US); MINAS GERAES: Caldas, 1867, Regnell 1390 (W); Antonio Justiniano, 17 km S of Oliveira, 16 Mar 1925, Chase 8900 (US); 1 km E of Itutinga along Hwy. 265 to Barbacena, 27 Feb 1976, Davidse & Ramamoorthy 10739 (MO); Lavras, 5 Mar 1925, Chase 8723 (MO, NY, US); Vicosa, 25 Apr 1925, Chase 9625 (F, MO, US); RORAIMA: Surumu Region, vicinity of Perreira Village, on an Azimuth of 356° 25' from Boa Vista, at a distance of 150 kms, 80 km NNE of Pereira Village, 27 Oct 1977, Coradin & Cordeiro 922 (US); SAO PAULO: Perus (cultivated), s.d., Usteri 21 (US); Horto Botanico (cultivated), Hammar 77 (US); Tremembe, 24 Jan 1922, Holway & Holway 1499 (US). BRITISH GUIANA. Rupununi Northern Savanna, 21 Aug 1963, Goodland & Maycock 499 (NY, US).

Sorghastrum contractum is characterized by the linear, dense or somewhat loose panicle, with the inflorescence branches ascending. In addition, this species has quite long awns (18-35 mm), however they are not as long as the awns of S. minarum.

Sorghastrum contractum grows in the tropical areas of the Americas. This species inhabits the northern and eastern zones of South America. In the northern regions the present species is reported only from British Guiana and the Brazilian State of Roraima. On the other hand, in the

Figure 41. Sorghastrum contractum. A. Basal part, bar=5 cm. B. Inflorescence, bar=5 cm. C. Ventral view of the spikelet, bar=1 mm

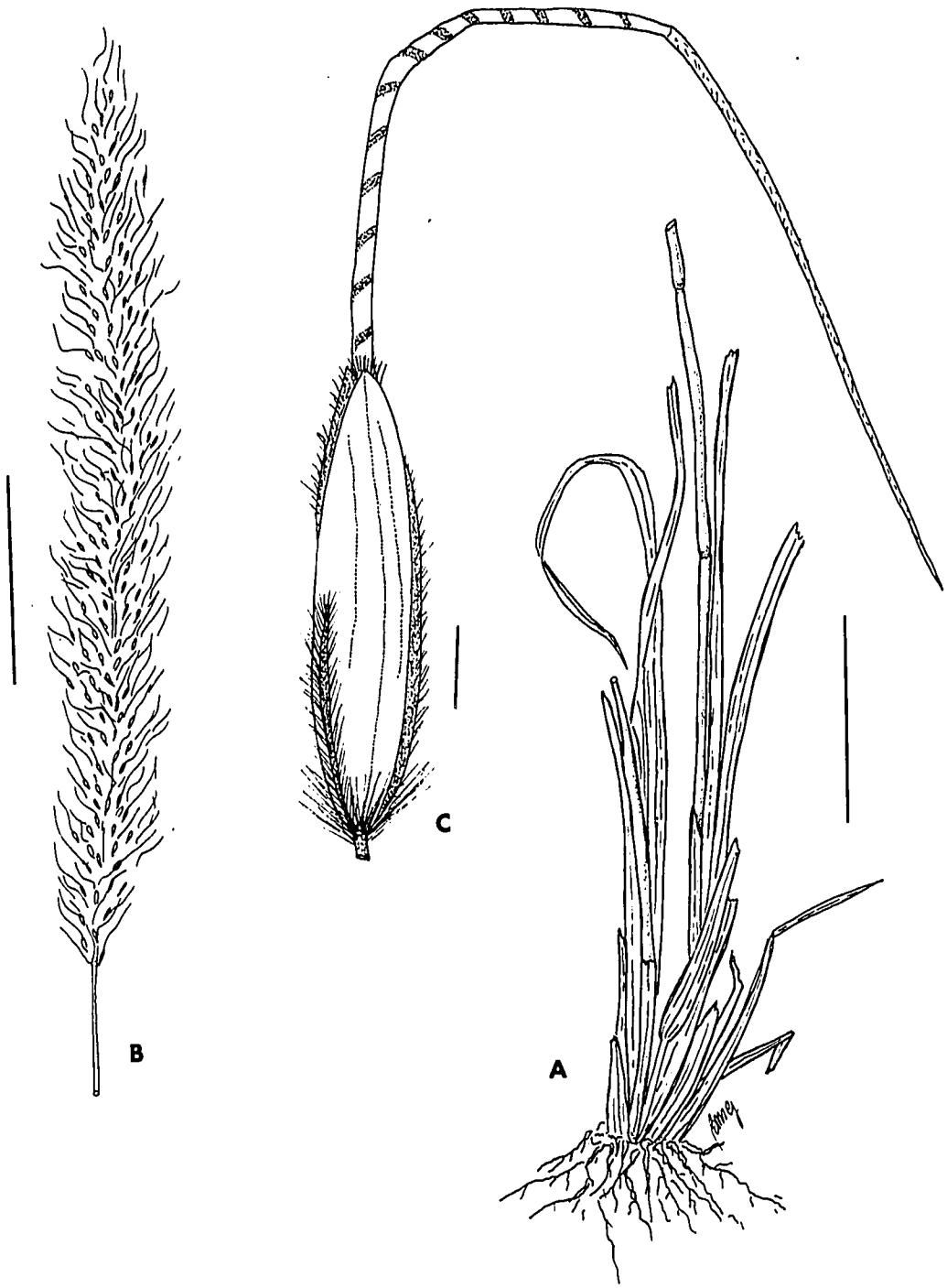

B
C
A

Figure 42. Distribution of Sorghastrum contractum


S. contractum
42
0
600 mi

eastern regions S, contractum occurs in Brazil, in the states of Minas Geraes, Mato Grosso, Sao Paulo and Roraima (Fig. 42).

Sorghastrum contractum is well adapted to open and rocky hillsides, savannas or grassland vegetation. This species has an altitudinal range from 100-1000 m. It occurs mainly at low elevations.

Sorghastrum contractum flowers from August to October in the Northern Hemisphere and from February to May in the Southern Hemisphere. In both cases, the flowering period takes place during the autumn season.

Sorghastrum contractum is related to Sorghastrum minarum. In both cases, the awn is quite long (the former has longer awns), and the spikelets have a sharp callus. Also these species are partially sympatric, which means that probably they have originated in the same area. Both prefer the same environmental conditions.

NOMENCLATURE:

Hackel (1883) included most of Sorghastrum species as different subspecies and varieties of Sorghum nutans. He suggested the name Sorghum nutans ssp. contractum for the present species. Hackel based his description on some specimens from Brazil. From these specimens, one from Lagoa Santa (Warning s.n.) was chosen as the lectotype for the present species. This specimen is deposited in (W).

In 1889 Hackel did not accept Sorghum nutans anymore. He included the Sorghastrum species as different varieties of Andropogon nutans. He proposed the new combination Andropogon nutans var. contractus.

Kuhlmann and Kuhn (1947), based on Nash's (1901) proposition of the new genus Sorghastrum, suggested the new combination Sorghastrum

contractum. This should be considered the legitimate name for the present species. Consequently, the basionym should be Sorghum nutans ssp. contractum and the lectotype should be represented by the specimen from Brazil deposited in (W), (Warning s.n.).

Swallen (1966) suggested the new species Sorghastrum amplum. It is based on a specimen from Sao Paulo, Brazil (Holway & Holway 1658), however, both the description and type fit within the present species.

5. Sorghastrum elliottii (Mohr) Nash, N. Am. Fl. 17:130. 1912. Chrysopogon elliottii Mohr, Bull. Torrey Club 24:21. 1897. Type: UNITED STATES. FLORIDA: 1884, Chapman 22 (Neotype: LP!). (Fig. 43A, 43B and 43C).

Andropogon nutans Elliott, Bot. S.C. and Ga. 1:144. 1816. Not A. nutans L. No specimen cited.

Sorghum nutans Chapman, Fl. S. U.S. 583. 1883. Not S. nutans (L.) Gray. No specimen cited.

Sorghum nutans ssp. linneanum Hackel, Fl. Bras. 2:276. 1883. Not S, nutans (L.) Gray. No specimen cited.

Andropogon nutans var. linneanus (Hackel) Hackel, DC. Monog. Phan 6:531. 1889. Not S. nutans (L.) Gray. Type: UNITED STATES. FLORIDA: 1884, Chapman 22 (Lectotype: LP!).

Chrysopogon nutans var. linneanus (Hackel) Mohr, Bull. Torrey Club 24:21. 1897. Based on Sorghum nutans ssp. linneanum Hackel.

Andropogon linneanus (Hackel) Scribner & Kearney, Bull. U.S. Dep. Agr. Agrost. 24:40. 1901. Based on Andropogon nutans var.

linneanus (Hackel) Hackel.

Sorghastrum linneanum (Hackel) Nash, Small Fl. SE U.S. 66. 1903. Based on Sorghum nutans Chapman.

Sorghastrum apalachicolense Hall, Sida 9(4):302. 1982. Type: UNITED STATES. FLORIDA: Liberty Co., at the jct. of Fl 12 and Fl 379, between Sumatra and Bristol, 5 Aug 1978, Godfrey 76630 (Holotype: FLAS!; Isotypes: MO, NY, US!).

Rhizome lacking. Culms erect to ascending, caespitose, (1.2-) 2-4 mm diam., 0.70-1.50 (-1.90) m tall. Internodes terete, smooth and glabrous. Leaves: blades flat to folded, 20-50 (-55) cm long, 2.5-5.5 (-8) mm wide, acute, scabrous and rarely pubescent above, scabrous below, margins serrulate; ligule decurrent, 2-4 (-5) mm long, ciliate; sheaths 15-30 (-45) cm long, (1.5-) 2-4.5 mm wide, generally glabrous, or pubescent at the margins in regions close to the ligule. Inflorescence an open panicle, erect or somewhat nodding, dark purple, 10-35 cm long; rachis terete, glabrous or scabrous; peduncle 20-55 (-65) cm long, glabrous. Spikelets dorsally compressed, lanceolate, deep chestnut brown at maturity, 6-7.5 mm long; callus 1-1.3 mm long, villous. Glumes obtuse, coriaceous; glume I truncate, 5.5-7 (-7.3) mm long, 1.5-2 mm wide, pubescent, 7-9-nerved; glume II acute, 6.2-7.5 mm long, 1.3-1.8 mm wide, glabrous, 5-nerved. Sterile Lemma bifid, hyaline, 4-6 mm long, 0.5-1.5 mm wide, ciliate, 2-nerved. Fertile lemma bifid, hyaline, 2-3-5 mm long, 0.5-1.2 mm wide, 3-nerved. Awn well developed, twice-geniculate, 25-40 mm long, 5 times longer than the spikelet. Anthers brownish, 2-3 mm long. Caryopsis reddish, 2-2.5 mm long. Sterile

Pedicel 3-6 (-6.5) mm long. Chromosome number 2n=20.

Representative specimens examined: UNITED STATES. ALABAMA: Mobile, Jul, Mohr s.n. (US); 3 miles from Creek Bridge, 18 Oct 1896, Mohr s.n. (US); Green Co., on Ala 14 toward Clinton, 8 Oct 1969, Kral 33895 (ISC); Lee Co., Auburn, 25 Sep 1897, Earle s.n. (NY); ARKANSAS: Sep 1886, Hasse 9027 (F); Jefferson Co., Watson State Park, 1 Oct 1942, Demaree 24057 (NY, US); DLEAWARE: Salisbury, Sep, Canby s.n. (US); FLORIDA: Apalachicola, Sep 1896, Chapman 4639 (NY, US); Apalachicola River, near Chattachoochee, 6 Oct 1939, Silveus 5364 (TEX); Calhoun Co., along Fla # 71, about 20 miles N of Wevahitchka, 20 Aug 1964, Henderson 64-488 (ISC); Hamilton Co., banks of Suwannee River, above Ellaville, 1 Oct 1955, Godfrey et. al. 53957 (NY); Hernando Co., section 25, T 21 S, R 19 E, Cooley et al. 7234 (US); Liberty Co., Torreya State Park, 15 Nov 1964, Godfrey 65015 (ISC); Leon Co., 2 miles E of Tallahassee, 23 Oct 1955, Godfrey 45295 (NY); GEORGIA: Crisp Co., 10 miles WSW of Cordele, 14 Oct 1967, Lane 1600 (NY); Elbert Co., along N side of Broad River at Anthony Shoals, 14.5 miles SE of Elberton, 1 Oct 1949, Duncan 10574 (ISC); Mcintosh Co., 3 miles N of S end and on inland side of Sapelo Island, 14 Oct 1956, Duncan 20642 (F, ISC, Tex); Sumter Co., Leslie, 7 Oct 1902, Harper 1718 (NY); INDIANA: Marshall Co., on the SW of Lake Mavinkuckee, 14 Sep 1921, Deam 34760 (US); LOUISIANA: Bienville Parish, roadside La. 507, 6 Oct 1971, Hunter 39 (F); Lincoln Parish, Hilly Fire Tower, near Hilly, 4 Oct 1972, Pavlu 71 (F); Washington Parish, 5 miles due W of Varnado (on Dollar Road), 1 Nov 1970, Thieret 32680 (LL); MARYLAND:

Salisbury, Sep 1872, Canby s.n. (F); MISSISSIPPI: near Biloxi, 5 Oct 1896, Kearney 305 (ISC); Pearl River Co., adjacent to Mississippi # 53, 10 miles Se Poplarville, 2 Sep 1964, Isely & Wemple 9100 (ISC); NORTH CAROLINA: Durham, 14 Oct 1940, Brown s.n. (TEX); Caswell Co., clearing on Lynch Creek, near N.C. Rt. 86, 2.2 miles SE of Hightowers, 29 Sep 1951, Fox 5451 (ISC); Chowan Co., 0.6 miles E of St. Johns on Indian Trail Road, 14 Oct 1958, Ahles & Duke 51013 (NY); Croven Co., Havelock, 20 Oct 1940, Brown 2325 (TEX); Martin Co., 4.5 miles NW Williamston, 30 Sep 1966. Radford & Bozeman 45281 (NY); Person Co., Loch Lily, Rozboro, 3 Sep 1937, Blomquist 9859 (F); Union Co., 1.8 miles S-SE of Waxhaw, 17 Sep 1957, Ahles 34047 (LL); Wilkes Co., 8 miles SW of Wilkesboro, hwy 18, 8 Sep 1937, Blomquist & Anderson 10013 (TEX); SOUTH CAROLINA: Greenwood Co., near S.C. 72, 8 miles NE of Greenwood, 13 Oct 1957, Radford 30867 (ISC); Lexington Co., Cayce, 5 Oct 1957, Radford 29763 (TEX); McCormick Co., 6 miles SW of McCormick, 18 Sep 1949, Duncan 10394 (ISC); TENNESSEE: Knoxville, Oct 1898, Ruth 21 (US); Cocke Co., along the French Broad River, between Pain Rock and Del Rio, 12 Sep 1897, Kearney 942 (NY, US); Knox Co., along Tennessee River, 4 miles SW from Knoxville, 23 Oct 1942, Iltis 1622 (LL, TEX); TEXAS: Texarkana, 15 Oct 1894, Letterman s.n. (F, ISC, MO, NY, TEX, US); Anderson Co., 6 miles NW of Tennessee Colony, 24 Sep 1953, Marsh 31 (TEX); Angelina Co., 2 miles E of Zavalla, 29 Sep 1967, Gould 12446 (TEX, US); Cass Co., about 6.5 miles S of Bivins, 18 Oct 1962, Correll 26417 (LL, NY); Gregg Co., 24 Aug 1941, York s.n. (MO, TEX); Harrison Co., Marshall. 17 Oct 1914, Palmer 6855 (MO, US); Henderson Co., 8 miles NW of Poynor, 20 Oct 1963, Correll 28557 (LL);

Houston Co., about 2 miles S of Grapeland, 2 Oct 1965, Correll & Correll 31788 (LL, NY); Jasper Co., 5 miles E of Jasper on U.S. 63, 27 Oct 1962, Johnston et al. 7045 (LL); Morris Co., 10 miles S of Daingerfield, 8 Oct 1937, Cory 25650 (US); Nacogdoches Co., 1959 clearcut strip plot B-4, 27 Sep 1961, Schuster 194 (TEX); Rusk Co., S of county, Oct 1950, Porter 51-1821 (TEX); Smith Co., Amigo, 19 Sep 1945, Moore 1041 (F, ISC, MO, NY, TEX, US); Tyler Co., 6 miles E of Woodville on FM 1746, 27 Oct 1962, Johnston et al. 6997 (LL); Upshur Co., 1.5 miles E of Big Sandy and 0.3 miles E of Sandy Creek, 26-27 Sep 1959, King 2205 (LL, TEX); VIRGINIA: W of Williamsburg, 19 Sep 1920, Chase 3056 (NY); Northampton Co., Cape Charles City, 8 Oct 1891, Canby s.n. (NY); Southampton Co., 7 miles S of Franklin, 7-8 Sep 1937, Fernald & Long 7312 (NY).

Sorghastrum elliottii is characterized by an open panicle, as well as the deep chestnut brown mature spikelets. It is distinguished from Sorghastrum brunneum which also has dark spikelets by its stouter aspect and longer awns and spikelets. In S. elliottii the awn is 5 times longer than the spikelet, meanwhile in S. brunneum the awns are 3.5 times longer than the spikelet.

Sorghastrum elliottii occurs in the southeastern and eastern United States (Fig. 44). It inhabits the lowlands surrounding the Appalachian Mountains. This species is distributed in the eastern coastal regions, in the states of Maryland, Virginia, North Carolina, South Carolina, Georgia and the Northern part of Florida (east of the Appalachian Mountains). It is also present in Alabama, Misssissippi, Louisiana and

Figure 43. Sorghastrum elliottii. A. Basal part, bar=5 cm. B. Inflorescence, bar=5 cm. C. Ventral view of the spikelet, bar=1 mm

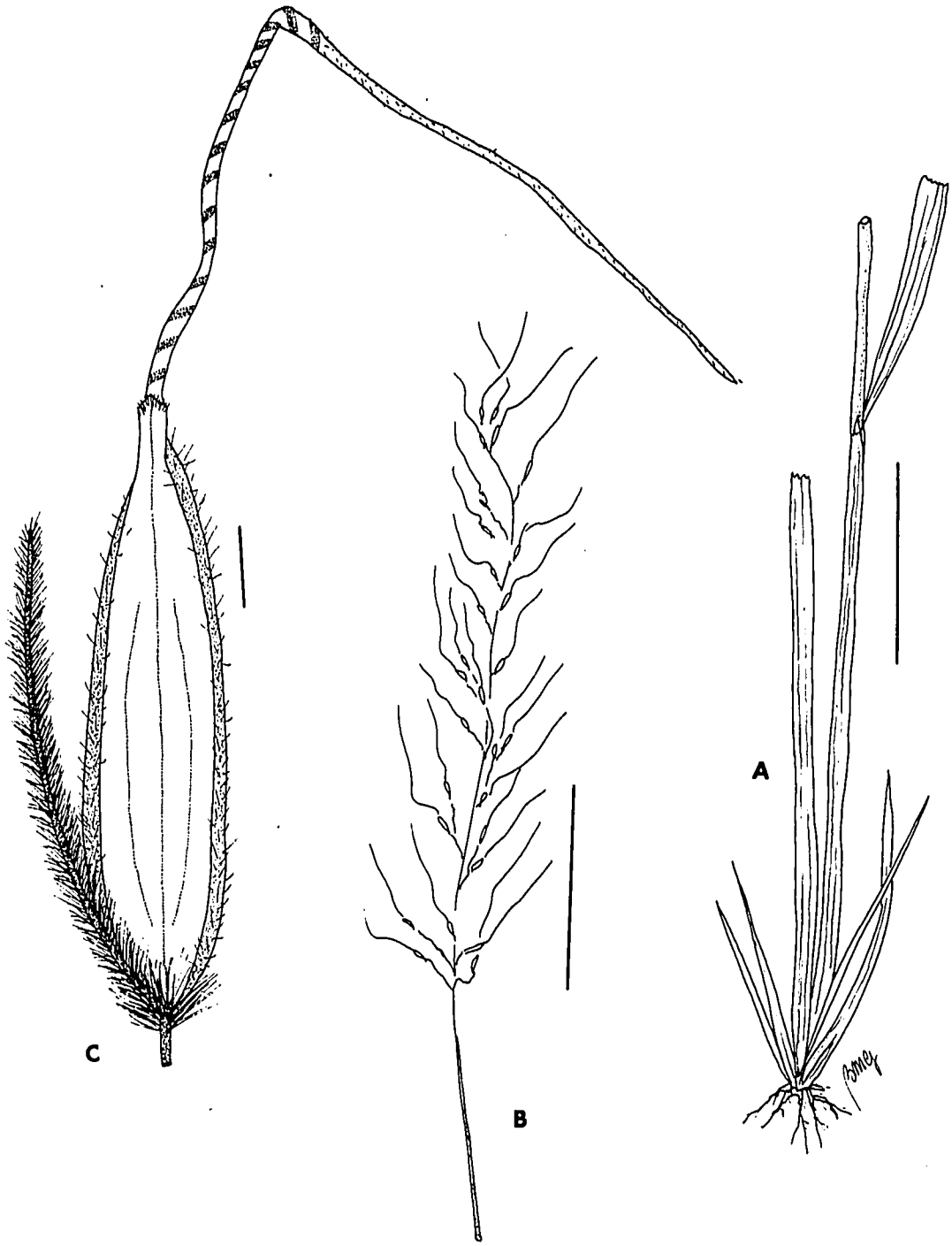

C
B
A

Figure 44. Distribution of Sorghastrum elliottii

S. elliottii

Texas (west of the Appalachian mountains), and finally in Arkansas and Indiana.

Sorghastrum elliottii usually inhabits dry, open woods, with sandy terraces. Is common along roads, trails or perturbed areas close to woodlands. This species usually flowers in autumn, during the months of August to October, rarely in June. The altitudinal range of the present species varies from sea level to less than 1000 m. However, this species always inhabits lowlands associated with the Appalachian Mountains. S. elliottii may be confused to Sorghastrum secundum to which it is related. S. elliottii has a lax and open panicle, with its branches distributed all around the inflorescence axis. On the other hand, S. secundum has a 1-sided panicle in which the branches usually form small clusters.

NOMENCLATURE:

When the species of Sorghastrum were included within the boundaries of Andropogon, Elliott (1816), cited Andropogon nutans L. as the name of the present species. Even though Elliott was referring to the present species by mentioning that his species was different from any other in the United States, the author misapplied the name Andropogon nutans L. No specimen was mentioned.

The same misapplication of the name took place by Chapman (1878). Chapman was referring to this species, mentioning its occurrence in dry barren soils of Florida. Again, no specimen was mentioned.

Hackel (1883) suggested the new combination Sorghum nutans ssp. linneanum. This author included most Sorghasstrum species as subspecies of Sorghum nutans. No specimen was cited. The same author in 1889,

decided to transfer the present species to the genus Andropogon. He proposed the name Andropogon nutans var. linneanus. In both combinations Hackel followed the former misapplications of Sorghum nutans L. by Elliott (1816) and Chapman (1878). However, for the first time some specimens are cited: Chapman, Florida; Reverchon, Texas; Liebmann 25, Haun., Mexico, Totutla).

Based on the fact that Chapman's specimen from LP is a duplicate from Hackel's Herbarium. I am designating this specimen as the Neotype for the present species. The herbarium label has the number "22" written on the upper left side, however, I am not sure if it is Chapman's collection number or something else.

Mohr (1897) did not include this species within Andropogon or Sorghum. Following Bentham (1881), he included it within the genus Chrysopogon, section stipoides. Furthermore, he split the present species, proposing Chrysopogon elliottii and Chrysopogon nutans ssp. linneanus. The author said that the former was characterized by a loose and more or less drooping panicle, whereas the latter was distinguished by having a weak and decumbent stem. In my opinion both "species" fit within the boundaries of the present species.

The new combination Andropogon linneanus, based on Hackel's name, was suggested by Scribner and Merrill in 1901. Both names represent synonyms of this species.

After Nash (1901) proposed the new genus Sorghastrum. He suggested the new combination Sorghastrum linneanum, which is based on Hackel's

names.

However, the ICBN (Stafleu, 1983) Art. 60.1, points out that in no case does a name have priority outside its own rank. This means that the epithet "linneanum" originally proposed by Hackel as a subspecies name, has no priority when raised to a specific rank. Nash (1903), based on this lack of priority, suggested the new combination Sorghastrum elliottii that is based on Chrysopogon elliottii Mohr.

Hall (1982) described the new species Sorghastrum apalachicolense as occurring on both sides of the Apalachicola River. Hall suggested that the panicle in S. apalachicolense is straight, whereas the panicle in S. elliottii is arching. Based on my morphological and anatomical studies I do not find characters to separate them.

In summary, based on the fact that the epithet "nutans" was misapplied; that the epithet "linneanus" does not have priority and that "apalachicolense" is a very recent name, the valid name for this species is Sorghastrum elliottii (Mohr) Nash. The basionym is Chrysopogon elliottii Mohr.

6. Sorghastrum incompletum (Presl) Nash (Figs. 45A, 45B and 45C)).

Rhizomes lacking. Culms erect or nodding, simple or branched, sometimes rooting from the basal nodes, 0.8-4 mm diam., 0.50-2 m tall, glabrous. Internodes terete, smooth, glabrous or slightly pubescent below the nodes. Leaves: blades linear, long attenuated at the apex, narrowed towards the base, 5-40 cm long, 1-10 mm wide, glabrous, rarely hairy, margins serrulate; ligule truncate, 1-3 mm long, scarious; sheath 5-30 cm long, 1-5 mm wide, tight, glabrous except in areas close to the

nodes, producing auricles along the ligules. Inflorescence loosely arranged or narrowly oblong, more or less nodding 10-40 cm long; rachis smooth and glabrous; peduncle 20-50 cm long, glabrous, smooth. Spikelets dorsally compressed, lanceolate, 4-6 (-7) mm long. Glumes coriaceous; glume I truncate, 3.5-5.5 (-6.5) mm long, 1-1.8 mm wide, ciliate at the lower half, 7-9-nerved; glume II lanceolate, acute, 3.5-5.5 (-7) mm long, 1-1.5 mm wide, glabrous, 5-nerved. Sterile lemma linear-oblong, hyaline, bifid, 2-4.5 mm long, 0.5-1.5 mm wide, ciliate, 2-nerved. Fertile lemma oblong, hyaline, bifid, 2-4 mm long, 0.5-1.5 mm wide, ciliate, 3-nerved. Awn twice geniculate, twisted, 1-4.5 cm long. Anthers 1-3.5 mm long. Caryopsis 1.5-3 mm long. Sterile Pedicel straight, 2.5-4.5 mm long, pubescent. Chromosome number 2n=20, 40.

6a. Sorghastrum incompletum (Presl) Nash var. incompletum. Andropogon incompletus Presl, Rev. Haenk. 1:342. 1830. Type: MEXICO. s.d., Presl s.n. (Holotype: US Fragm.!).

Andropogon galeottii Fournier, Mex. Pl. Gram. 56. 1881. Type: MEXICO. VERACRUZ: Zacuapan, Jun-Oct 1840, Galeotti 5698 (Lectotype: BR!); Zoquitlan pres Orizaba, 19 Oct 1865-1866, Galeotti 2269 (Syntype: BR!).

Sorghum canescens Hackel, Mart. Fl. Bras. 23:277. 1883. Type: BRAZIL. GOYAZ: Villa Boa, s.d., Pohl 2819 (Holotype: W!; Isotypes: W!).

Andropogon nutans L. var. incompletus (Presl) Hackel, DC. Monogr. Phanerog. 6:531. 1889. Based on Andropogon incompletus Presl.

Sorghastrum liebmannianum Hitchcock, Contr. U.S. Natl. Herb. 17(3):211. 1913. Type: MEXICO. VERACRUZ: Orizaba, open rocky hill, 24 Aug 1910, Hitchcock 6352 (Holotype: US!; Isotype: NY!).

Sorghum incompletum (Presl) Stapf, Fl. Trop. Afr. 9(1):145. 1919. Based on Andropogon incompletus Presl.

Sorghastrum galeottii (Fournier) Conzatti, Fl. Taxonomica Mexicana 1:170. 1946. Based on Andropogon galeottii Fournier.

Culms slender, shorter than var. bipennatum, 0.8-2 (-2.5) mm diam., 0.50-1 (-1.30) m tall. Inflorescence loosely arranged, but sometimes narrowly oblong, glaucous or greenish, seldom dark. Spikelet 4-6 (-9) mm long. Awn twice geniculate, twisted, 10-35 mm long, 4-6 times longer than the spikelet.

Representative specimens examined: COLOMBIA. 5 miles S of Mamatoca, 21 Nov 1898-1899, Smith 139 (NY); ARAUCA: Corregimiento de Cravo Norte, region de Cano Rico, 20 Jan 1955, Gomez 24 (US). COSTA RICA. CARTAGO: 3 km E of Paraiso, above waterfall Catarata Los Novios, 1 Nov 1968, Pohl & Davidse 11396 (ISC, US); GUANACASTE: 5 km S of Liberia along the Carretera Interamericana, 5 Dec 1968, Pohl & Davidse 11550 (F); PUNTARENAS: 3 km N of the Carretera Interamericana, along the road to Boruca, 12 Dec 1968, Pohl & Davidse 11589 (F). GUATEMALA. CHIMALTENANGO: along road to San Martin Jilotepeque, 25 Nov 1938, Standley 57964 (US); JUTIAPA: between Jutiapa and La Calera, SE of Jutiapa, 2 Nov 1940, Standley 76142 (US); SANTA ROSA: Naranjo, Nov 1892, Heyde & Lux 3929 (US). HONDURAS. EL PARAISO: road to Danli, 1 Nov 1951, Swallen 11197 (ISC); MORAZAN: Zamorano, 15 Nov 1945, Valerio 3577

(US); drainage of the Rio Yeguare, 8 Dec 1949, Williams 17019 (US); OLANCHO: Jutiapa, Forest Camp, near Salama, 21 Dec 1978, Pohl 13743 (ISC, MO). MEXICO. CAMPECHE: carretera Nunkkni-Hacienda Santa Cruz, Km 4, Laikini, 20 Nov 1985, Ortiz 939 (XAL); CHIAPAS: 7 km N of Tuxtla Gutierrez along road to El Sumidero, 16 Oct 1965, Breedlove & Raven 13380 (ENCB, US); 2 Km al S de Teopisca, 33 km al SE de San Cristobal, 23 Oct 1985, Davila et al. 194 (ISC); 40 km al NO de San Cristobal de Las Casas, 24 Oct 1985, Davila et al. 196 (ISC); COLIMA: Tuxpan Canyon, 3 Nov 1910, Orcutt 4707 (MO); ESTADO DE MEXICO: Temasclatepec, 13 Oct 1932, Hinton 2069 (US); Tonatico, 26 Sep 1954, Matuda 31727 (US); GUERRERO: Achotal, Sep 1926, Reko 4994 (US); 5 miles N of Ocotito on the Chilpancingo-Acapulco Hwy., near both Agua del Obispo and Acahuizotla, 4 Nov 1960, Johnston & Crutchfield 5983 (US); HIDALGO: Molango, May 1937, Gossweileri 1269 (US); JALISCO: steep mountainsides, 4.5 miles N-NE of Talpa de Allende, 12-14 Oct 1960, McVaugh 20202 (NY); Mun. de Tecatitlan, Barranca de San Juan de Dios, cerca de Los Corales, 23 Oct 1963, Rzedowski 17394 (ENCB); 1 km al O de la carretera Ayutla-Mascota, en la desviacion a Cuautla, 16 Nov 1985, Davila & Lot 206 (ISC); 2.4 km al NO de la Primavera, sobre la carretera Ayutla-Talpa de Allende, 16 Nov 1985, Davila & Lot 207 (ISC); MICHOACAN: 1.2 miles E of Tuxpan on Mex. 15, 20 Oct 1976, Brunken & Perino 442 (CHAPA); MORELOS: Cuernavaca, 29 Oct 1903, Holway 5269 (NY); Yautepec, 1935, Gandara 19 (US); NAYARIT: camino de San Pedro Lagunillas a la Laguna, 21 Oct 1981, Real 326 (COT); steep treeless hills, 10 miles SE of Tepic, 2 miles SE of El Refugio, 6 Oct

1952, McVaugh 13381 (US); OAXACA: from Temascalapa to San Ildefonso de Villa Alta, Dtto. de Villa Alta, 29-30 Oct 1944, Vera 3548 (US). NICARAGUA. Grenada, 1868, Flint s.n. (US). PANAMA: along the old Las Cruces trail, between Fort Clayton and Corozal, 3 Dec 1923, Standley 29072 (US); along Rio Dupi, eastern Chiriqui, 19 Dec 1911, Pittier 5227 (NY). SALVADOR. near San Salvador, 1923, Calderon 1439 (NY, US). VENEZUELA. COJEDES: llanura Contigua al sur de Las Galeras de El Pao, nov 1981, Ramia & Gil 7535 (VEN); 21 km W de San Carlos, along Hwy. 5, 17 Nov 1971, Davidse 3138 (US, VEN); PORTUGUESA: 20 km NE of Guanare, along Hwy. 5, 17 Nov 1971, Davidse 3151 (ISC).

Sorghastrum incompletum var. incompletum grows in the tropical areas of the Northern Hemisphere of the New World (Fig. 46). This variety ranges from the Sierra Madre Occidental, in the Mexican state of Nayarit, through Guatemala and Panama, up to the northern Andean Mountains of Colombia and Venezuela. The absence of this variety from the southern regions of Venezuela and from Brazil is probably due to the presence of lowlands (Llanos and Cerrados), typical of those regions. Sorghastrum incompletum var. incompletum is also absent in the Southern Andean regions.

Sorghastrum incompletum var. incompletum flowers from September to December, during the autumn season. This variety is well adapted to median-high altitudes (500-2500 m).

Figure 45. Sorghastrum incompletum. A. Basal part, bar=5 cm. B. Inflorescence, bar=5 cm. C. Ventral view of the spikelet, bar=1 mm

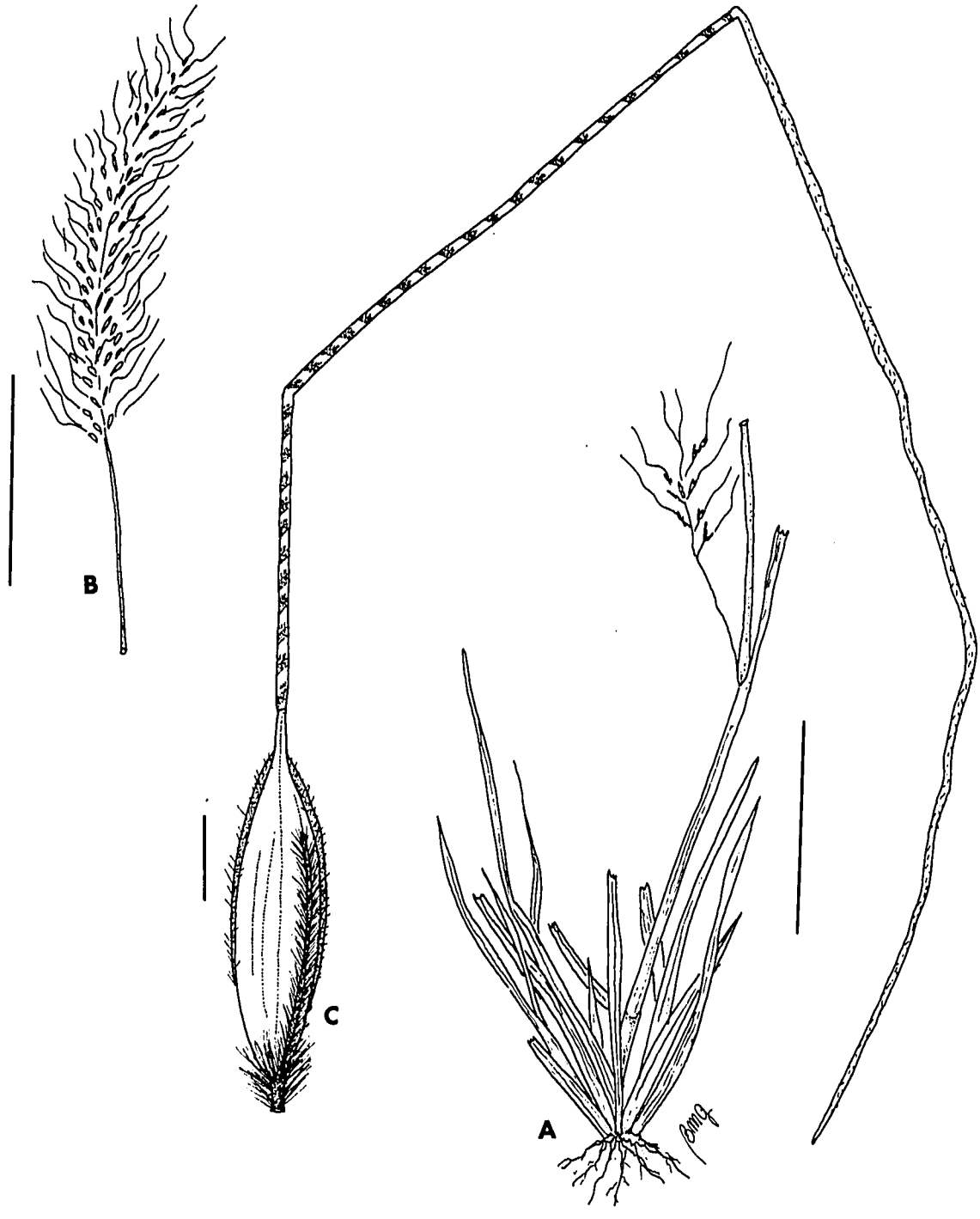
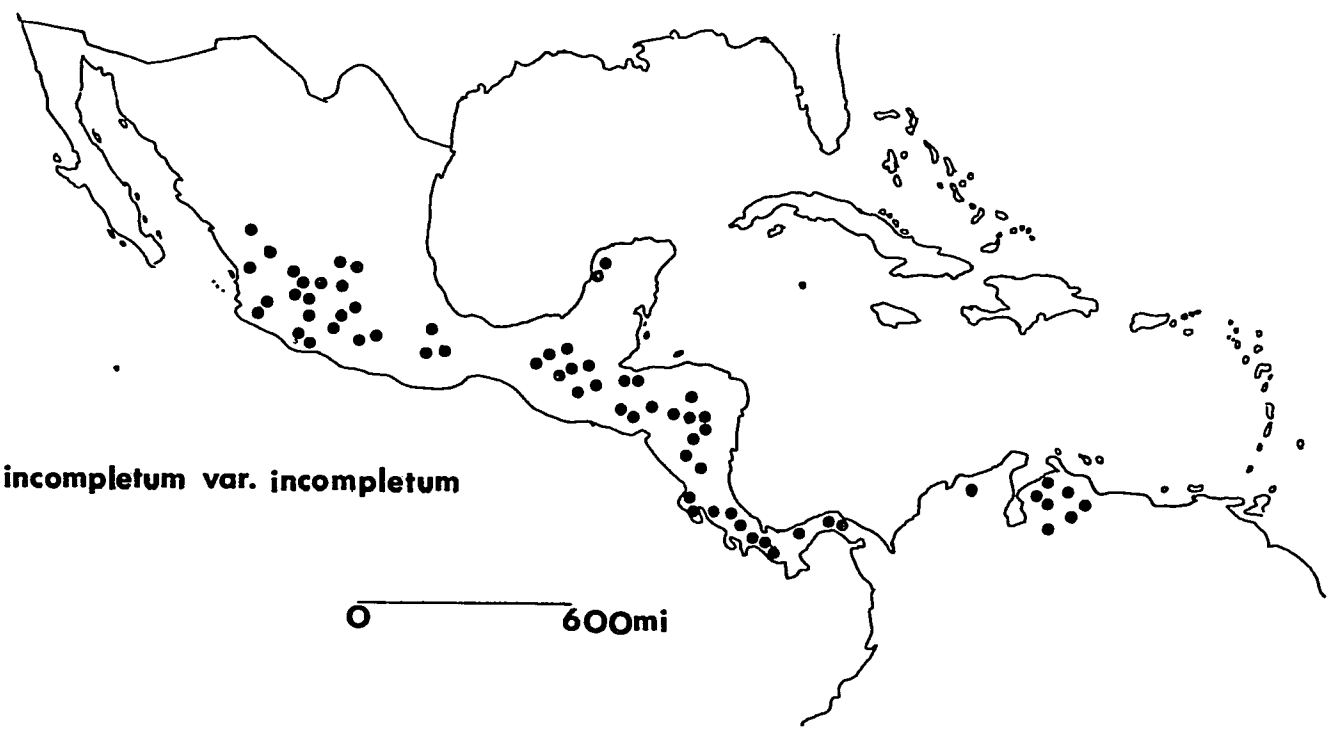

B
C
A

Figure 46. Distribution of Sorghastrum incompletum var. incompletum



(46)

NOMENCLATURE:

As is usual in Sorghastrum history, the genus was included within Andropogon sensu lato. Presl (1830) cited Andropogon incompletum based on a specimen from Mexico and with unknown locality. This name, as well as the specimen, are considered respectively the basionym and the holotype of Sorghastrum incompletum var. incompletum.

Due to the wide distribution range of the species, many "regional" species names were published. Fournier (1881) proposed the name of Andropogon galeottii for a Mexican population of this species, in Veracruz state. Even though, the description and the specimens of Fournier fit with S. incompletum, he failed by confusing the present species with Andropogon stipoides HBK (Sorghastrum stipoides). However, in his synonym citation, Fournier mentions the name Andropogon stipoides Rupr., because Ruprecht (1842) helped in the identification of this and other species.

A new combination was proposed when Hackel (1883), based on a specimen from Goyaz, Brazil, suggested the name Sorghum canescens. However, the original description as well as the type specimen fit with those found in the present species.

The same author, Hackel (1889), transferred this species to the genus Andropogon. He suggested the name Andropogon nutans var. incompletus for the present species.

After the genus Sorghastrum was proposed by Nash in 1901, he proposed the new combination Sorghastrum incompletum in 1912. This should be considered the legitimate name for the present species, and

subsequently the basionym is Andropogn incompletus Presl.

Hitchcock (1913) suggested the new species Sorghastrum liebmannianum. It is based on a Mexican specimen (Hitchcock 6352). However, the description and type specimen fit with Sorghastrum incompletum.

Two other new combinations were cited for the present species. First, Stapf (1919) did not accept the genus Sorghastrum and proposed the name Sorghum incompletum. Then, Conzatti (1946) suggested the combination Sorghastrum galeottii. In both cases, they represent synonymns of Sorghastrum incompletum.

6b. Sorghastrum incompletum (Presl) Nash var. bipennatum (Hackel) Davila. Comb. nov. Andropogon bipennatus Hackel, Androp. Nov. Fl. 68(8):142. 1885. Type: Central African Republic. Djur and Scriba Ghattas, 12 Oct 1869, Schweinfurth 2486 (Holotype: US!).

Sorghum bipennatum (Hackel) Kuntze, Rev. Gen. Pl. 2:791. 1891. Based on Andropogon bipennatus Hackel.

Sorghum bipennatum (Hackel) Stapf, Fl. Trop. Afr. 9:144. 1934. Based on Andropogon bipennatus Hackel.

Sorghastrum bipennatum (Hackel) Pilger, Notzbl. Bot. Ber. 14(121):96. 1938.

Culms stouter than variety incompletum, 2-4 (-1) mm diam., 0.80-1.70 (-2) m tall. Inflorescence very lax, dark. Spikelet 4-6 mm long. Awn twice geniculate, twisted, 35-45 mm long, 7-9 times longer than the spikelet.

Specimens examined: ANGOLA. HUAMBO: Regio Huambo-Benguela, Chianga-Nova Lisboa, Jul 1948, Baptista 14175 (US); MALANGE: Kamba, Kamana-Malange, Jun 1925, Gossweiler s.n. (US). BURUNDI. BURURI: Butare (Mosso), 2 Jun 1977, Reekmans 6319 (ISC, MO). CAMEROON. Yaounde, 1894-1895, Staudt & Yenker 561 (US). DEMOCRATIC REPUBLIC OF THE CONGO. Kitobes (Congo Belge), 19 May 1910, Flamigni 183 (US); Kitobes (Congo Belge), 1910, Flamigni 349 (US); Sumba, Jando, 14 May 1924, Gossweiler 8944 (US). GHANA. Bolgatanga-Nvoronga, 19 Oct 1954, Mensah 488 (US); 12 miles N of Ejura, 15 Nov 1970, Hall & Duodo s.n. (MO); Gold Coast, Jogo, near Chindire, Nov 1948, Harold 263 (US); near Navrongo, N. Terr., Oct 1938, Vigne 203 (US). GUINEA. Balanki, 16 Jan 1951, Roberty 13521 (MO); BEYLA: Kerovane, 15 Nov 1949, Adam 7022 (MO); Konsankoro, 20 Nov 1949, Adam 8444 (MO); MACENTA: Diaradou, 10 Nov 1949, Adam 6962 (MO). IVORY COAST. Odienne, 10 Oct 1943, Adam 27188 (MO). NIGER. Park "W" Niger, West Africa, 16 Oct 1975, Hempe 132 (MO). NIGERIA. ABEOKUTA: Egba District, one mile from Olokemeji Stn., 9 Nov 1944, Douchie F.H.T.8145 (MO, US). PORTUGUESE GUINEA. Bafata, Contubo-El., 18 Nov 1945, Junhv 3601 (MO). SENEGAL. TAMBACOUNDA: Niokolo-Koba, 19 Nov 1958, Adam 15591 (MO); Sinthiou-Maleme, 31 Nov 1956. Adam 13887 (MO). SIERRA LEONE. KABALA: Sekurela, 15 Nov 1965, Adam 21968 (MO). TANZANIA. KILOSA: Mugira Track, s.d., Greenway & Kanuri 15464 (MO); Mtwara: 140 km W Lindi, Rondo Plateau, 20 Apr 1935, Scheieber 6321 (B); SONGEA: Songea, 4 May 1956, Milne-Redhead & Taylor 9884 (US). UPPER VOLTA. 15 km W of Bobo-Dioulasso, 13 Oct 1967, Geerling & Bokdam 1279 (MO); Creek bottom, 7 km E-SE of Boromo, 27 Oct 1972, Sihvonen 76 (MO).

Sorghastrum incompletum var. bipennatum differs from variety incompletum by having a looser and darker panicle. Also, variety bipennatum has longer awns, as well as longer awn/spikelet proportion than variety incompletum. Finally, S. incompletum var. bipennatum is confined to Africa, whereas S. incompletum var. incompletum occurs in the Americas.

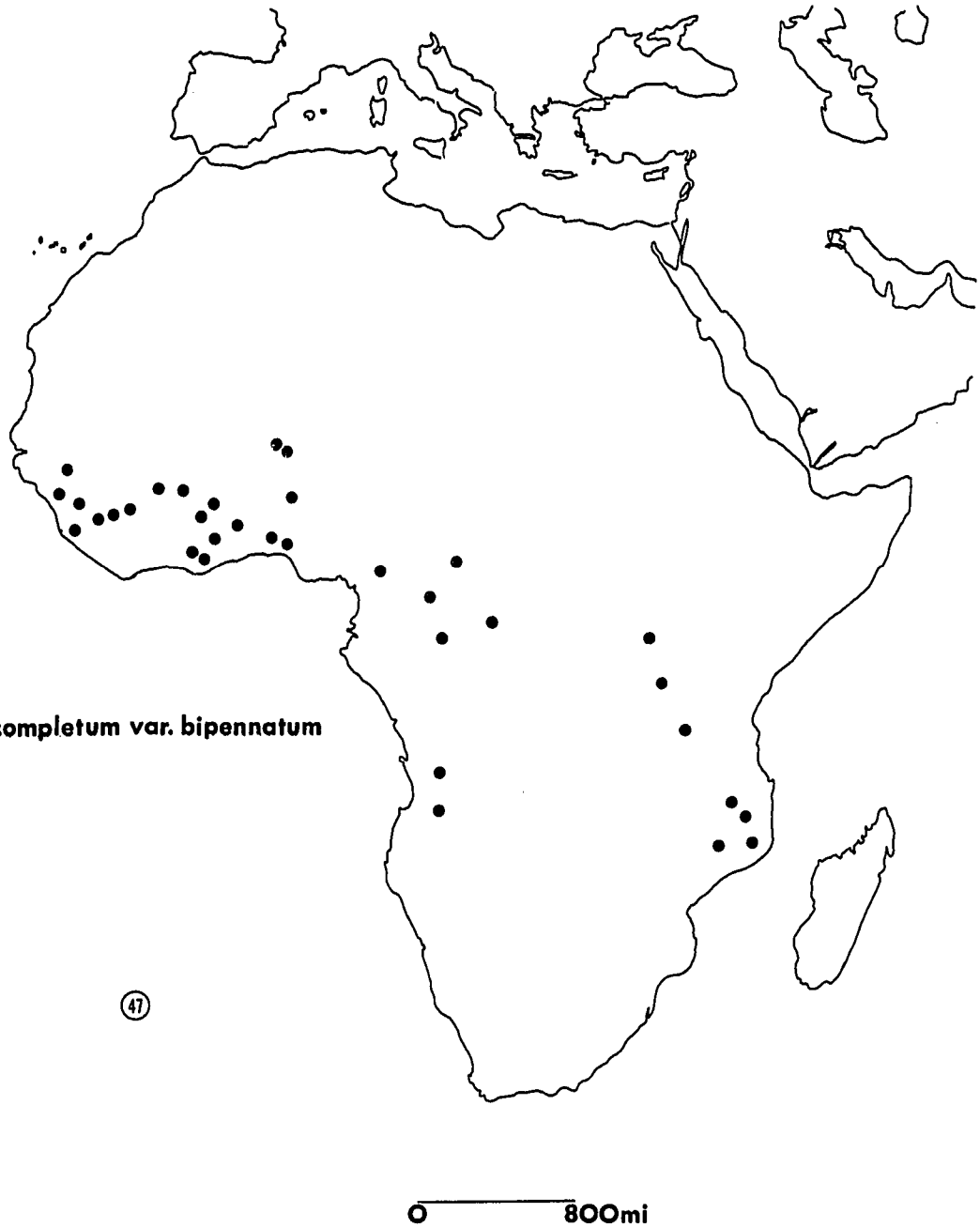
Sorghastrum incompletum var. bipennatum grows in tropical areas of Africa. It is present in the Sudano-Zambesian and Guineo Congo regions, where a savanna type of vegetation is dominant (Fig. 47).

The southernmost populations of this variety flower from May to June (Angola, Burundi, Democratic Republic of the Congo and Tanzania). On the other hand, the Northern populations flower from September to December (Cameroon, Ghana, Guinea, Ivory Coast, Niger, Nigeria, Portuguese Guinea, Sierra Leone and Upper Volta). In both cases, the flowering period corresponds to the autumn season.

The altitudinal range for S. incompletum var, bipennatum varies from 500-1500 m. It is associated with the lower parts of the African mountains.

Sorghastrum incompletum is related to S. chaseae. These two species posses unique and very distinctive characteristics within the genus. S. chaseae shows a clambering habit and S. incompletum is the only annual species.

Figure 47. Distribution of Sorghastrum incompletum var. bipennatum


S. incompletum var. bipennatum
47
0
800mi

NOMENCLATURE:

Hackel (1885) included the genus Sorghastrum within the boundaries of Andropogon. He proposed the name Andropogon bipennatus, based on a specimen from The Central African Republic (Schweinfurth 2486).

Kuntze (1891) did not accept the present species as belonging to the genus Andropogon, but to the genus Sorghum. He suggested the new combination Sorghum bipennatum.

In 1934, Stapf, probably ignoring Kuntze's combination, suggested again the same name Sorghum bipinnetum.

After the genus Sorghastrum was proposed by Nash (1901), Pilger (1938) suggested the combination Sorghastrum bipennatum.

This taxonomic entity of Africa differs from the entity of the Americas only in the awn length. For this reason, I prefer to think that both entities are varieties belonging to the species Sorghastrum incompletum.

Final Considerations

Sorghastrum incompletum is an annual or short-lived perennial species. Within the individuals of this species, variation can be seen mostly in height, inflorescence shape and color, as well as in the awn length. With respect to the reminder of the morphological features, their ranges overlap very frequently, and no real distinction is apparent.

Even though many overlapping features are shown by Sorghastrum incompletum and Sorghastrum bipennatum, I decided to transfer S. bipennatum as a variety under S. incompletum, instead of reducing it to a

synonym under S. incompletum. Two reasons support this decision. Firstly the awn in S. incompletum is always shorter than the awn of S. bipennatum and; secondly, their distribution pattern is disjunct.

In relation with the awn length, the S. bipennatum awn is 7-9 times longer than the spikelet, while in S. incompletum the awn is 4-6 times longer than the spikelet. It is important to point out that in both groups, the spikelets are similar in shape and size.

The awn is an accessory structure attached to the seed, dealing with the function of a "drill" mechanism that helps in the establishment of a new plant (Stebbins, 1974). This function becomes important when recalling that one of the weakest stages in a plant life cycle is the establishment of the seedling. For this reason the awn function of moving the fruit to a favorable microsite, orientating it to facilitate initial water uptake and anchoring it (Peart, 1984), has important evolutionary and adaptative significance. Stebbins (1974) mentions that the perfection of the awn drill mechanism is associated with the further occupation of relatively dry habitats.

I am accepting these two varieties, not because the differences in awn length, but because of the differences in the proportions between awn and spikelet length, as a way of measuring the ability to settle down in much drier environments for those individuals having a much greater difference in awn/spikelet proportion, i.e., Sorghastrum incompletum var. bipennatum.

In relation with their disjunct distribution pattern, Sorghastrum

incompletum grows in woodland edges and savanna types of Mexico, Central America, and Northern South America. On the other hand, Sorghastrum bipennatum is well represented in the Sudano-Zambesian and Guineo-Congo regions (Brenan, 1978). For the understanding of this distribution pattern, four main observations have to be taken in consideration. Firstly, it is especially difficult to determine for widespread species, whether they are native or introduced in a given area (Clayton and Renvoize, 1986; Thorne, 1973). Secondly, most of the grasses, even though well equipped for dispersal, are not able to cross oceans (Clayton and Renvoize, 1986). Thirdly, many of the species common to Africa and America are maritime plants of shallow salt water, salt marshes, salinas, mangrove swamps, dunes, etc. (Thorne, 1973); finally, it is expected that indigenous species of both Africa and America are plants that can be dispersed by birds or water over large distance.

Analyzing these four statements with the exception of the lack of information for answering the first one, it is assumed that this species neither is well adapted for travelling transoceanic trips, nor inhabits wet places or is dispersed by birds. This probably means that Sorghastrum incompletum, originated somewhere in Africa or in the Americas and was probably introduced to the counterpart lacking this species. However, the awn length difference along with its function already discussed, make me think that certain degree of differentiation between the two isolated populations of S. incompletum has occurred.

7. Sorghastrum minarum (Nees) Hitchcock, Contr. U.S. Natl. Herb. 24:501. 1927. Trachypogon minarum Nees, Agrost. Bras. 349. 1829. Type: BRAZIL: Prov. Minarum, between Villa Rica and Tejuco, Itambe (Holotype: US fragm.!). (Figs. 48A, 48B and 48C).

Andropogon minarum (Nees) Kunth, Rev. Gram. 1:507. 1830. Based on Trachypogon minarum Nees.

Stipa penniglumis Trinius, Mem. Ac. St. Petersb. 1:77. 1833. No type specimen cited.

Sorghum minarum (Nees) Hackel, Fl. Bras. 2:276. 1883. Based on Trachypogon minarum Nees.

Chrysopogon minarum (Nees) Bentham, Linn. Soc. 9:73. 1881. Based on Trachypogon minarum Nees.

Rhizome lacking. Culms erect, 2-4 mm diam., 0.80-1.50 m tall. Internodes terete, generally smooth, glabrous or slightly pubescent below the node. Leaves: blades flat or slightly convolute, 20-40 cm long, 4.0-7.5 mm wide, apex acute, glabrous, margins serrulate; ligule 3.0-4.0 (-4.5) mm long, glabrous; sheaths 15-30 cm long, 2.5-4 (-5.8) mm wide, glabrous or slightly pubescent at the ligular area. Inflorescence strict and erect panicle, 10-25 cm long; rachis terete, glabrous; peduncle 35-45 cm long, glabrous. Spikelets dorsally compressed, lanceolate, 5.5-7 mm long; callus sharp, 2.5-3 mm long, silky villous. Glumes coriaceous; glume I truncate, 5-6.5 mm long, 1-1.2 (-1.5) mm wide, pubescent, 7-9-nerved; glume II 5.5-7 mm long, 1-1.2 (-1.5) mm wide, glabrous, acute, 5-nerved. Sterile lemma linear, hyaline, bifid, (3-) 4-5 mm long, (0.6-) 1-1.4 mm wide. Fertile lemma linear-oblong, hyaline, bifid, 3.0-4.2 mm

long, 0.5-1 (-1.2) mm wide. Awn twice-geniculate, twisted, 6-8.5 cm long, 11 or more times longer than the spikelet. Anthers 2-2.5 mm long. Caryopsis brownish, 3-3.5 mm long. Sterile Pedicel 3-4.5 mm long, pubescent. Chromosome number 2n=20.

Specimens examined: ARGENTINA. CORRIENTES: Dtto. Bellavista, 19 km S de Bellavista, Est. Cuevas, 24 May 1973, Schinnini 6537 (CTES); Dtto. Empedrado, Arroyo Gonzalez y Ruta 12, 27 Feb 1974, Quarin et al. 2233 (CTES, US); Dtto. Mburucuya, Santa Cruz, 24 Feb 1951, Pederson 1033 (US). BOLIVIA. Tunaria, s.d., Kuntze s.n. (NY); BENI: Near Reyes, Apr 1947, Cutler 9081 (US). BRAZIL. s.d., Sellow 1184 (US); Mun. Lajes, Morro Pinheiro Seco, 3 km E of Lajes, 16 Mar 1957, Smith & Klein 12216 (NY, US); BRASILIA: s.d., Riedel s.n. (NY); Chapada de Contagem, cerrado and margin of Lagoa Paranda, 2 Feb 1968, Irwin et al. 19462 (F, MO, NY); MARANHAO: Mun. de Loreto, Ilha de Balsas, region between the Rios Balsas and Parnaiba, 18 km S of Loreto, 12 Apr 1962, Eiten & Eiten 4272 (US); MINAS GERAES: 30 km SW of Campanha, along Hwy. 267 to Sao Paulo, 25 Feb 1976, Davidse & Ramamoorthy 10627 (LL, MO); MATO GROSSO: 12 km W of Campo Grande, 7-11 Feb 1930, Chase 10870 (F, NY, US); PARANA: Capao Grande, 3 Mar 1904, Dusen 4024 (US); Ponta Grossa, Estacao Experimental, 2 Feb 1946, Swallen 8401 (US); SANTA CATARINA: Abelardo Luz, 28 Feb 1964, Klein 4889 (US); Curitibanos, 22 Feb 1962, Reitz & Klein 12301 (NY, US). PARAGUAY. Cordillera de Altos, Cerro Coihe, 23 Feb 1903, Fiebrig 779 (F, SI, US); central Paraguay, 1888-1890, Morong 488A (F, US).

Sorghastrum minarum is easily distinguished by having the longest

awn of all species of the genus, as well as by showing a very sharp callus. The awn is usually twice-geniculate, brownish and twisted. Also, the present species has a dense and brush-like inflorescence. Spikelets of S. minarum are sometimes confused with spikelets of some species of Stipa due to the pungent callus, however in S. minarum, the sessile spikelet has a very conspicuous pedicel (rudiment of the pedicelled spikelet) attached to the base.

Sorghastrum minarum is distributed in South America in the countries of Argentina, Paraguay, Bolivia and Brazil (Fig. 49). This species has an altitudinal range from 200-1000 m. It occurs mainly at low elevations, but associated with the mountain chains.

Sorghastrum minarum is well adapted to dry sandy pastures, as well as eroded and altered places. It flowers mainly from January to March, but some individuals flower in April. This corresponds to the autumn in the Southern Hemisphere.

Sorghastrum minarum is similar to Sorghastrum tisseranti, proposed by Clayton in 1975. Principally, the similarities deal with the large size of the awns, the pungence of the sessile spikelet and the shape of the inflorescence. However, based on the lack of specimens of S. tisseranti (just the type specimen has been seen), this species is considered doubtful until further specimens become available.

Probably S. minarum is related to S. balansae. In both cases the awn is quite long and the spikelets have a pointed callus. Also, these species are partially sympatric, which means that probably both have originated in the same area and also that both prefer the same

Figure 48. Sorghastrum minarum. A. Basal part, bar=5 cm. B. Inflorescence, bar=5 cm. C. Ventral view of the spikelet, bar=1 mm

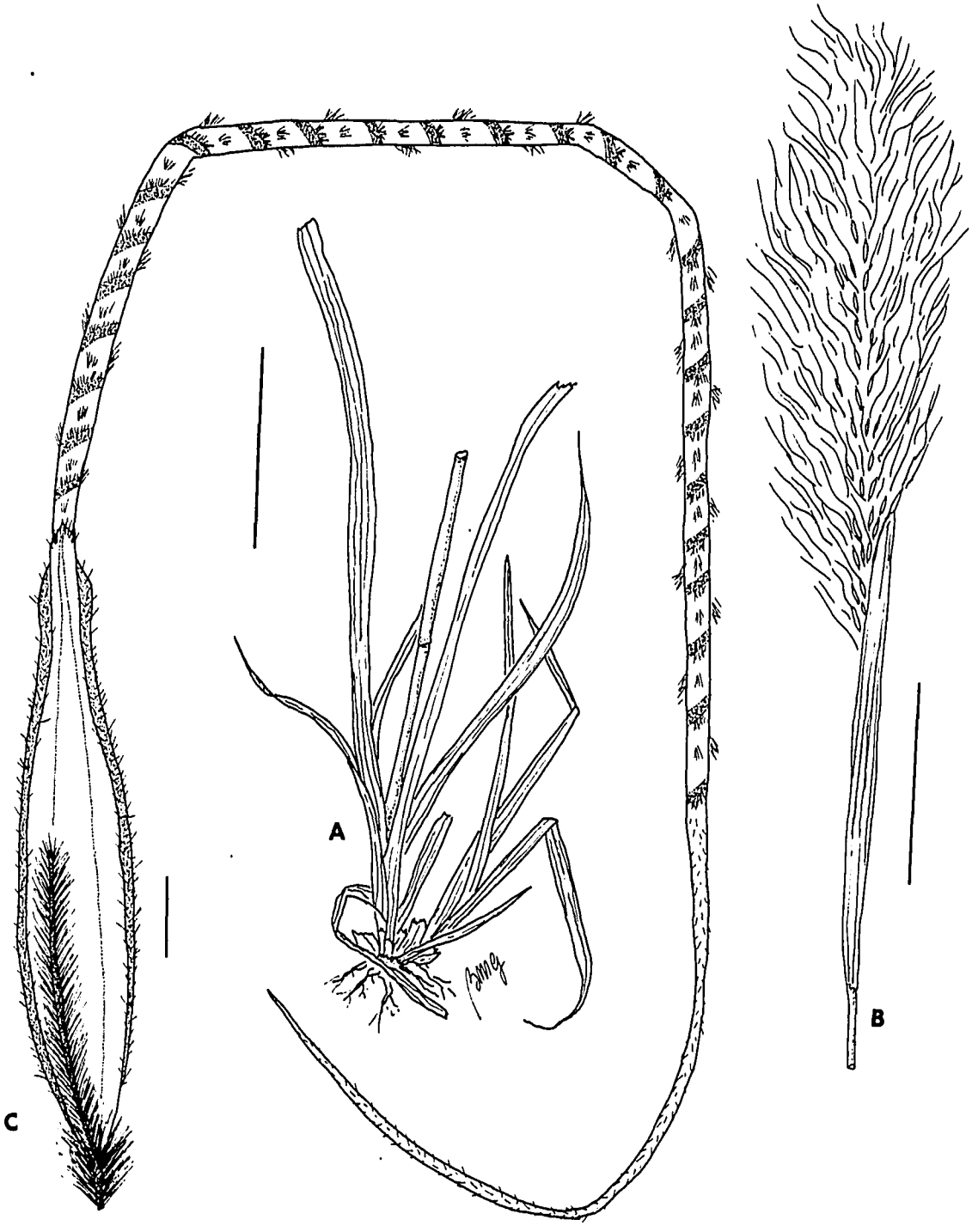

A
B
C

Figure 49. Distribution of Sorghastrum minarum


S. minarum
49
0
600 mi

environmental conditions.

NOMENCLATURE:

Nees (1829) included the present species, as well as other species of Sorghastrum, within the limits of the genus Trachypogon. He proposed the name Trachypogon minarum based on a specimen from Brazil (Villa Rica and Tejuco). This name is the basionym of Sorghastrum minarum and subsequently the specimen from Brazil should be the type specimen.

Kunth (1833) suggested the inclusion of the present species within Andropogon. Based on Nees name, he proposed the name Andropogon minarum.

Stipa penniglumis was another name applied to this species. It was proposed by Trinius in 1831, and probably this misidentification is due to the resemblance of these two genera with respect to their large awns, and pungent callus.

Hackel (1883) transferred this species to Sorghum. He suggested the name Sorghum minarum, based on Trachypogon minarum.

Bentham (1881) did not accept the inclusion of the present species in either Andropogon or Sorghum. He suggested the name Chrysopogon minarum, which again is based on Trachypogon minarum.

Finally, after Nash (1901) proposed the genus Sorghastrum, Hitchcock (1927) suggested the new combination Sorghastrum minarum, which should be considered the legitimate name for this species.

8. Sorghastrum nudipes Nash, N. Amer. Fl. 17. 129. 1912. Type: MEXICO. CHIHUAHUA: pine plains, base of the Sierra Madre, 18 Sep 1887, Pringle 1433 (Holotype: NY!; Isotypes: F!; US!). (Figs. 50A, 50B and 50C).

Rhizomes present. Culms slender, tufted, with many short extravaginal innovations, 1-1 (-2.5) mm diam., 0.55-0.90(-1.10) m tall. Internodes terete, smooth and glabrous. Leaves: blades erect, flat, apex acute 10-30 cm long, 2-5 (-7) mm wide, usually glabrous, sometimes rough and pubescent, margins serrulate: ligule decurrent, 15-25 mm long; sheaths smooth and glabrous, pubescent close to the ligular areas in immature individuals, 7-20 (-30) cm long, 1-2 (-3) mm wide. Inflorescence panicle loose and open, broad, the capillary branches and their divisions naked below the middle, few spikelets borne at their ends, 10-30 cm long; rachis terete, glabrous; peduncle 15-30 (-50) cm long, glabrous. Spikelets lanceolate, dorsally compressed, 5.5-7.5 (-8.5) mm long; callus villous. Glumes 2, chartaceous-coriaceous; glume I truncate, 5.5-7.5 (-8) mm long, (1.2-) 1.4-1.8 mm wide, pubescent, usually 7-9-nerved, seldom more than 9 nerves; glume II acute, (5.4-) 6-7 (-8.5) mm long, 1.2-1.8 mm wide, generally glabrous, sometimes pubescent in the lower half, 5-nerved. Sterile lemma hyaline, bifid, (4.9-) 5-6.5 mm long, 0.5-1.7 mm long, ciliate, 2-nerved. Fertile lemma hyaline, bifid, 35-55 mm long, 0.5-1 (-1.5) mm wide, ciliate, 3-nerved. Awn straight or sometimes once-geniculate, 12-18 (-23) mm long, usually 2-2.5 times longer than the spikelets. Anthers 3-4 mm long. Caryopsis 2-3 mm long. Sterile Pedicel 3-6 mm long, pubescent. Chromosome number 2n=20. Specimens examined: MEXICO. CHIHUAHUA: 1937, Le Seur 187 (US); base of Sierra Madre, 10 Oct 1888, Pringle 1692 (BAB); southwestern Chihuahua, Aug-Nov 1885, Palmer 11 (NY, US); Chuhuichupa, Aug-Sep 1930, Le Sueur 086

(MO, TEX, US); Sierra Madre mountains, near Colonia Garcia, Townsend & Barber 336 (MO, TEX, US); camino Guachochic-Creel, 5 km antes del entronque a la Bufa, 24 Sep 1981, Siqueiros 1616 (COT); 16 km al E de la desviacion a la Bufa, en el camino Guachochic-Creel, 25 Sep 1985, Davila et al. 137 (ISC); 7 km al NO del entronque de la Bufa y el camino que va de Guachochi-Creel, 26 Sep 1985, Davila et al. 143 (ISC); 6 km al NO de Kirare, en el camino de Guachochi-Bufa, 25 Sep 1985, Davila et al. 142 (ISC); Guicorichi, Rio Mayo, 7 Oct 1935, Gentry 1965 (US); Sanchez, 12 Oct 1910, Hitchcock 7678 (ISC, US); Mun. Cusihuiriachic, Rancho El Coronel, 2 Sep 1981, Loya & Mendez 1516 (COT); Mun. Moris, 13 Sep km al N de El Pilar, brecha a Yecora, 30 Sep 1985, Tenorio et al. 10085 (MEXU); Mun. Norogachic, 12 km al NE de Norogachic, en el pueblo de Tucheachi, 24 Sep 1985, Davila et al. 132 (ISC); Mun. Ocampo, Cascada de Basaseachic, 26 Sep 1985, Tenorio et al. 9968 (MEXU); Mun. Temosachic, Canon Huahuatan, 10 miles SE of Madera, 22 Sep 1939, Mueller 3410 (F, LL, MO). DURANGO. El temascal, 4 km al So de Piedra Herrada, Mun. Suchil, 11 Sep 1981, Gonzalez 1973 (CHAPA). SONORA. Cochuto, 4 Oct 1890, Hartman 88 (US); Sierra Tecurahui, southeastern part of the state, 26-28 Oct 1961, Gentry et al. 19398 (LL); Mun. Yecora, 12 km al O de El Talayote, 30 Sep 1985, Tenorio et al. 10125 (MEXU).

Sorghastrum nudipes is characterized by a slender habit. The panicle is loose, open and broad. The inflorescence branches are very slender, bearing few spikelets that are borne at their ends. The awn usually is straight, but sometimes geniculate. A very distinctive character of S. nudipes is the presence of many short extravaginal

Figure 50. Sorghastrum nudipes. A. Basal part, bar=5 cm. B. Inflorescence, bar=5 cm. C. Ventral view of the spikelet, bar=1 mm

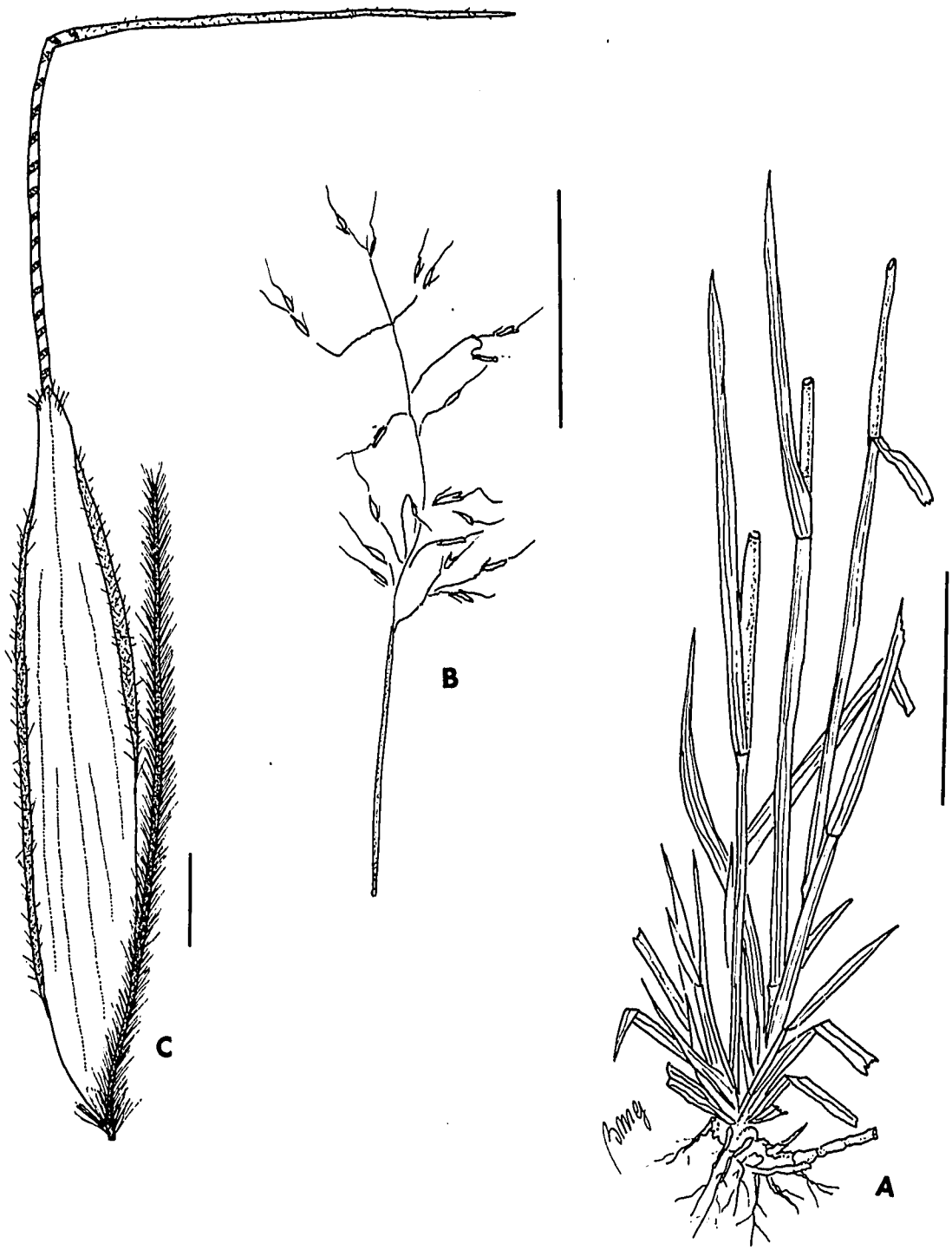
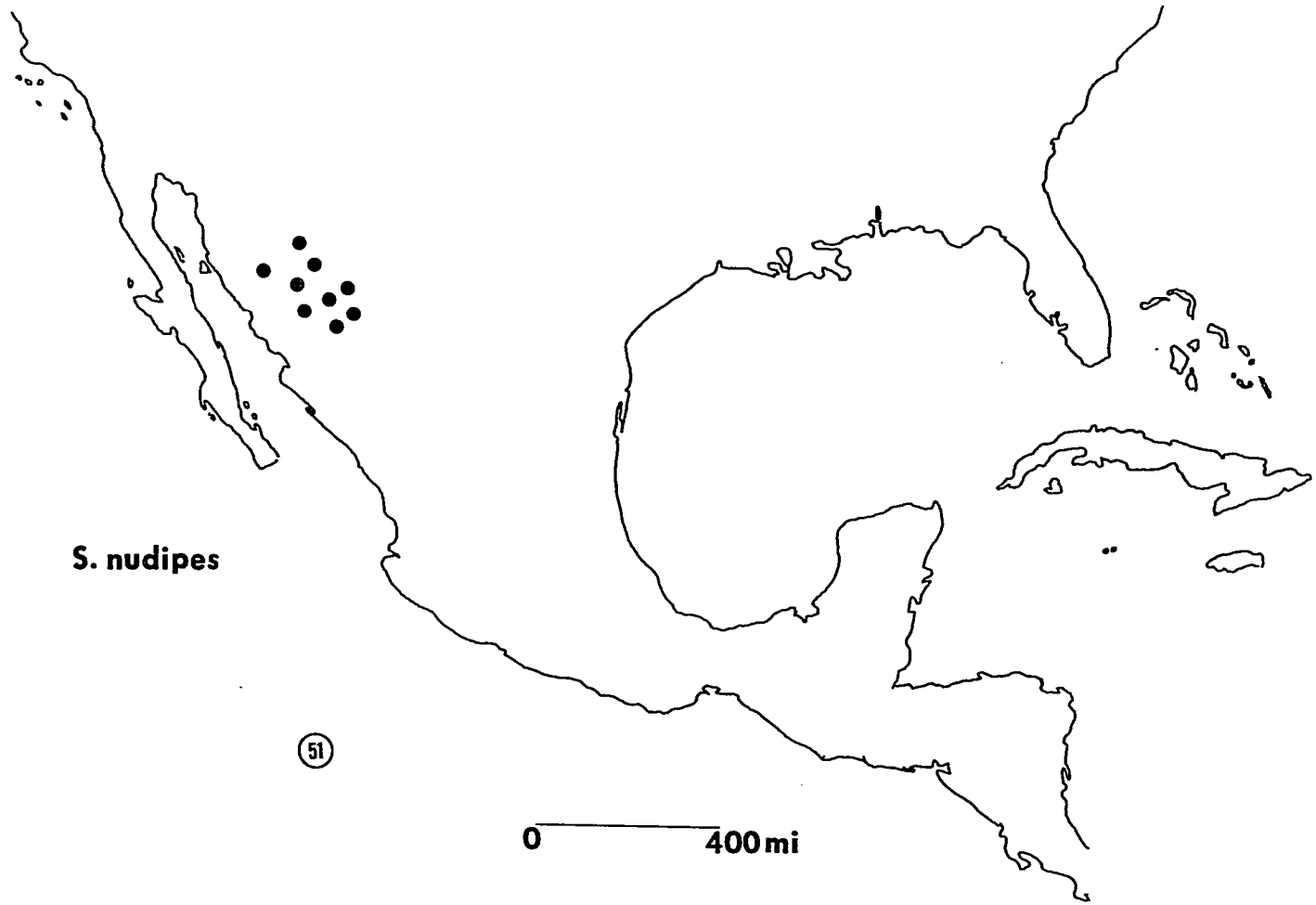

C
B
A

Figure 51. Distribution of Sorghastrum nudipes


S. nudipes
51
0
400 mi

innovations.

Sorghastrum nudipes is distributed in the northeast of Mexico in the states of Chihuahua, Sonora, and Durango (Fig. 51). It inhabits medium altitudes zones, along the Sierra Madre Occidental. It occurs from the Sierra Tarahumara, in Sonora and Chihuahua, to the Sierra de Topia in Durango. Probably S. nudipes may be present in Zacatecas.

Sorghastrum nudipes inhabits pine plains, pine-oak woods, rocky slopes and argillaceous soils. It flowers at the end of the summer and the beginning of the autumn. The altitudinal range for this species is from 1000-3000 m.

Sorghastrum nudipes is probably related to Sorghastrum nutans. The lengths of their spikelets and awns are very similar (the largest spikelets among Sorghastrum species). However, the inflorescence shape is quite different. In S. nutans the inflorescence is dense and crowded, whereas in S. nudipes the inflorescence is loose and open and the spikelets are located at the tips of the branches.

9. Sorghastrum nutans (L.) Nash, Fl. SE U.S. 66. 1903. Andropogon nutans L., Sp. Pl. ed. 1. 1045. 1753. Type: UNITED STATES. VIRGINIA: s.d., Clayton 621 (Holotype: BM; US Photo 76596 !; Microfiche Linn. Soc. London!). (Figs. 52A, 52B and 52C).

Andropogon avenaceus Michaux, Fl. Bor. Amer. 1:58. 1803. Type: UNITED STATES. ILLINOIS: s.d., Michaux s.n. (Holotype: P Photo!).

Andropogon ciliatus Elliott, Sk. Bot. S.C. and Ga. 1:144. 1816. Type: UNITED STATES. SOUTH CAROLINA: Dry pine-barrens on Port Royal, s.d., s.c. (Holotype: CHARL?).

Sorghum nutans (L.) Gray, Man. Bot. U.S. 617. 1848. Based on Andropogon nutans L.

Chrysopogon nutans (L.) Bentham, J. Linn. Soc. Bot. 19:73. 1881. Based on Sorghum nutans (L.) Gray.

Chrysopogon avenaceus (Michaux) Bentham, J. Linn. Soc. Bot. 19:73. 1881. Based on Andropogon avenaceus Michaux.

Sorghum avenaceum (Michaux) Chapman, Fl. South U.S. 583. 1883. Based on Andropogon avenaceus Michaux.

Sorghum nutans (L.) Gray ssp. avenaceum var. genuinum Hackel, Fl. Bras. 2. 1883. Based on Andropogon avenaceus Michaux.

Andropogon albescens Fournier, Mex. Pl. 2:56. 1881. Type: MEXICO. VERACRUZ: 1867, Gouin 53 (Holotype: P!).

Andropogon confertus Trinius, Mex. Pl. 2:55. 1881. Type: UNITED STATES. TEXAS: s.d., Berlandier 1873 (Holotype: G!).

Andropogon nutans L. var. avenaceus (Michaux) Hackel, DC. Monogr. Phan. 6:530. 1889. Based in Andropogon avenaceus Michaux.

Chrysopogon nutans (L.) Bentham var. avenaceum Coville & Banner, Rep. Geol. Surv. Ark. 4: 234. 1891. Based on Chrysopogon nutans (L.) Bentham, and on Chrysopogon avenaceus (Michaux) Bentham.

Poranthera nutans (L.) Rafinesque ex Jacks, Ind. Kew 2:606. 1894. Based on Andropogon nutans L.

Poranthera ciliata (L.) Rafinesque ex Jacks, Ind. Kew 2:606. 1894. Based on Andropogon ciliatus Elliott.

Sorghastrum avenaceum (Michaux) Nash, Man. Fl. U.S. & Can. 71.

1901. Based on Chrysopogon avenaceus Bentham.

Chalcoelytrum nutans (L.) Lunell, Amer. Mid. Natl. 4:212. 1915. Based on Sorghastrum nutans (L.) Nash.

Sorghastrum albescens (Fournier) Beetle, Phytologia 52(1):17. 1982. Based on Andropogon albescens Fournier.

Rhizome present, scaly, stout and short. Culms erect, 1.5-4.5 mm diam., (0.50-) 0.70-1.80 (-2.35) m tall. Internodes terete, smooth and glabrous. Leaves: blades long, linear, flat, tapering to a narrow base, 10-50 (-70) cm long, 1-4 mm wide, apex attenuate, rarely pubescent, margins serrulate; ligule membranous, usually developing thickened and pointed auricles, 2-5 (-6) mm long; sheaths 10-40 (-50) cm long, 2-5 (-7) mm wide, glabrous or sometimes slightly hispid. Inflorescence a loosely contracted panicle, yellowish or brownish, rather dense, 10-35 cm long; rachis terete, hirsute; peduncle 20-60 (-75) cm long, glabrous. Spikelets dorsally compressed, light brown to straminous, 5-8 (-8.7) mm long; callus blunt, villous. Glumes coriaceous, glume I truncate, 50-70 (-80) mm long, 1-1.8 mm wide, pubescent, 7-9-nerved; glume II acute, (40-) 50-80 mm long, 1-1.8 mm wide, glabrous, 5-nerved. Sterile lemma bifid, hyaline, 4-6 (-7) mm long, 0.5-1.8 mm wide, ciliate, 2-nerved. Fertile lemma bifid, hyaline, 3-5.5 mm long, 0.5-2 mm wide, 3-nerved. Awn geniculate, tightly twisted below the bend, 10-22 (-30) mm long, about 2-3 times longer than the spikelet. Anthers (2-) 3-5 mm long. Caryopsis 2.3 mm long. Sterile Pedicel 3-6 mm long, pubescent. Chromosome number 2n=20, 40, 80.

Representative specimens cited: CANADA. ONTARIO: Sauble Beach, 16 Aug

1934, Krotkov 8732 (NY); QUEBEC: Pontiac Co., Bristol, 20 Sep 1938, Senn 810 (NY); MEXICO. CHIAPAS: S of the Center of Amatenango del Valle, Mun. of Amatenango del Valle, 5 Sep 1966, Shilom 1069 (NY); along Mexican Hwy. 190, 3 miles S of La Trinitaria, Mun. La Trinitaria, 15 Aug 1965, Breedlove 11771 (TEX, US); NW edge of Teopisca, along Mexican Hwy. 190, Mun. Teopisca, 25 Jun 1965, Breedlove 10538 (ENCB, TEX, US); CHIHUAHUA: Rancho Exp. La Campana, 82 kms al N de la cdad. de Chihuahua, 26 Aug 1978, Fernandez s.n. (ENCB); COAHUILA: Muzquiz, Palm Canyon, 19 Sep 1936, Marsh 986 (TEX); 1 km al S del Casco del Rancho El Bonito, Canon El Bonito, Mun. Acuna, 27 Aug 1985, Davila et al. 89 (ISC); ESTADO DE MEXICO: 5 km W de Progreso Industrial, 18 Sep 1977, Rzedowski 35291 (ENCB); near Villa Guerrero, cerro del Aguila, 25 Sep 1980, Beetle M-5809 (COT); GUANAJUATO: carr. La Piedad-Cd. Manuel Doblado, Mun. Penjamo, 17 Sep 1981, Santillan 0221-R (COT); Km 6, carr. Apaseo El Alto-Jerecuaro, Mun. de Apaseo El Alto, 29 Aug 1981, Mora 27-AMB (COT); GUERRERO: Zihuagio, 16 Oct 1936, Hinton 9700 (LL); JALISCO: Rio Blanco, 1886, Palmer 511 (US); Guadalajara, side of Barranca Oblatos, 27 Sep 1910, Hitchcock 7346 (US); 11 miles S of Talpa de Allende, road to La Cuesta, 15 Oct 1980, McVaugh 20245 (NY, TEX); Sierra del Tigre, 2 miles NE of Mazamitla, 23 Sep 1952, McVaugh 13192 (US); MICHOACAN: vicinity of Morelia, NW de Panguato, 26 Sep 1909, Arsene 2675 (NY); 39 miles W of Morelia, 29 Oct 1960, Johnston 5926 (US); 18 miles from Jiquilpan, on the road SW to Colima, 30 Oct 1960, Crutchfield & Johnston 5930 (TEX, US); between Rio del Salto and La Polvilla, 18 miles E of Morelia, 9 Nov 1961,

King & Soderstrom 5069 (NY, TEX); Cerro Potrerillos, 5 miles N of Cotija and 22 miles S of Jiquilpan Alotepec, rumbo a Zapotitlan, 27 Oct 1979, Guerrero 403 (COT); NAYARIT: Socoro Island, Mar-Jun 1897, Anthony 401 (US); Socorro Island, 29 Mar 1931, Howell 8449 (F, US); OAXACA: 19 km de Miahuatlan, 29 Oct 1979, Guerrero 425 (COT); TAMAULIPAS: Mun. Villa Casas, on the road from Ramcho Las Yucas to Santa Maria de los Nogales, 22 Sep 1956, Martinez & Borja F-1987 (US); VERACRUZ: 25 Aug 1867, Gouin 324 (MO); Alta Luz, Sep 1912, Purpus 5592 (NY, US); Alta Luz, Sep 1907, Purpus 2897 (US); ZACATECAS: 1 km al NO de Tanque de los Rayos, Mun. de Valparaiso, cerca de San Francisco, 3 Nov 1963, Rzedowski 17640 (ENCB). UNITED STATES. ALABAMA: Clair Co., summit of Beaver Creek, 10.5 miles N of Fall City, 1 Oct 1971, Kral 44628 (MO); ARIZONA: Chicahwa Mts., Pine Canon, 25 Sep 1896, Toumey 17 (US); ARKANSAS: Logan Co., S slopes of Magazine Co., 9 Nov 1925, Palmer 29518 (US); COLORADO: Marshall, 19 Aug 1901, Ramaley 624 (ISC); CONNECTICUT: New London Co., vicinity of Latimer's Point, Fisher's Island Sound, 1.5 miles SE of Mystic, 9 Sep 1979, Hill 8745 (NY); DELAWARE: Greenback, 28 Aug 1882, Commons 149 (US); GEORGIA: Oglethorpe Co., Echols Mill, about 9.3 miles N of Lexington, Piedmont Province, 23 Oct 1965, Blake & Montgomery 269 (F); ILLINOIS: Peonia Co., Sep 1903, McDonald s.n. (NY); Lake Co., Waukegan, N of City limits, vicinity between Sheridan Rd. and Northwestern Railroad, 31 Jul 1977, Pinette 1933 (ISC); INDIANA: Wells Co., Jackson, 15 Sep 1901, Deam s.n. (US); IOWA: Clayton Co., Mc Gregor, 21 Jul 1925, Pammel 909 (ISC); KANSAS: Miami Co., 1885, Oyster 3643 (NY); KENTUCKY: Bell Co., Sep 1893, Kearney 384 (F); LOUISIANA: Covington, Sulphur

Spring, Oct 1919, Arsene 11562 (US); MASSACHUSETTS: Hampshire Co, North Maple St., Florence, 4 Sep 1973, Ahles 78630 (ISC); MICHIGAN: Flint, 19 Aug 1909, Sherff s.n. (F); MINNESOTA: Glenwood, Aug 1891, Taylor s.n. (NY); Greene Co., vicinity of Strafford, 27 Aug 1912, Standley 9477 (US); MISSISSIPPI: near Ocean Springs, 6 Oct 1896, Kearney 294 (US); Stackville, 27 Sep 1896, Kearney 30 (US); NEBRASKA: 10 miles S of Valentine, 28 Aug 1958, Thieret 4557 (F); NEW JERSEY: Somerset Co., Watchung, 27 Aug 1930, Moldenke 1371 (MO); NEW MEXICO: Sierra Co., Kingston, Aug 24 1904, Metcalfe 1242 (US); NEW YORK: Nassan Co., Hempstead Plains, 2.3 miles SE of Westbury, 3 Oct 1916, Pennell 9332 (NY); NORTH CAROLINA: Orange Co., 3 miles E of Hillsboro, 29 Sep 1939, Blomquist 10944 (F); NORTH DAKOTA: Benson Co., Butter, 25 Aug 1915, Lunnell s.n. (US); OHIO: Auglare Co., St. Mary's, 25 Sep 1900, Natzein 6779 (US); OKLAHOMA: Harper Co., 10 miles S of Buffalo, 21 Oct 1941, Smith 79 (TEX); PENNSYLVANIA: barrens of Huntington Co., Sep 1874, Courie s.n. (F); RHODE ISLAND: Cumberland, 13 Sep 1903, Greenman 1800 (MO); SOUTH CAROLINA: Chesterfield Co., Sandhills Wildlife Refuge, McBee, 2 Dec 1940, Hopkins 25 (US); SOUTH DAKOTA: Bell Fourche, 4 Aug 1897, Griffiths 396 (US); TENNESSEE: Blount Co., Sep 1897, Ruth 246 (NY); TEXAS: Sabine Co., 11 miles S of Yellowpine, 27 Oct 1962, Johnston 7099 (LL); Wise Co., Post Oak Belt, 13 miles W of Rhome, 4 Nov 1947, Whitehouse 19228 (NY); VIRGINIA: Fairfax Co., 6 Sep 1933, Allard 49 (F); VERMONT: Charlotte, Essex, 18 Aug 1877, Horsford s.n. (F); WISCONSIN: Marinette Co., Aug 8 1933, Grassi 2991 (NY); WYOMING: Laramie Co., Jul

1900, Nelson 331 (US).

Sorghastrum nutans is distinguished by having a dense and somewhat nodding inflorescence, as well as by showing very long spikelets (up to 9 mm long). This species may be confused with S. setosum, however, the spikelets in the latter reach no more than 5 mm long and usually have a small awn.

Sorghastrum nutans is distributed in the Southern regions of Canada, and is widespread in the United States, except for the northwest corner of the country. The western limits of S. nutans in the U.S. are the Rocky Mountains. Probably this natural barrier has stopped the further migration of S. nutans to the western regions. It also occurs in Mexico, from Coahuila and Chihuahua, extending to Jalisco, Michoacan, Oaxaca and Chiapas. It occurs mainly across the Sierra Madre Occidental, but it also occurs at the Sierra Madre Oriental, in Tamaulipas state (Fig. 53). Furthermore, it occurs in The Revillagigedo Islands in the Pacific Ocean. However, I think that the presence of this species on these islands is due to introduction rather than natural establishment.

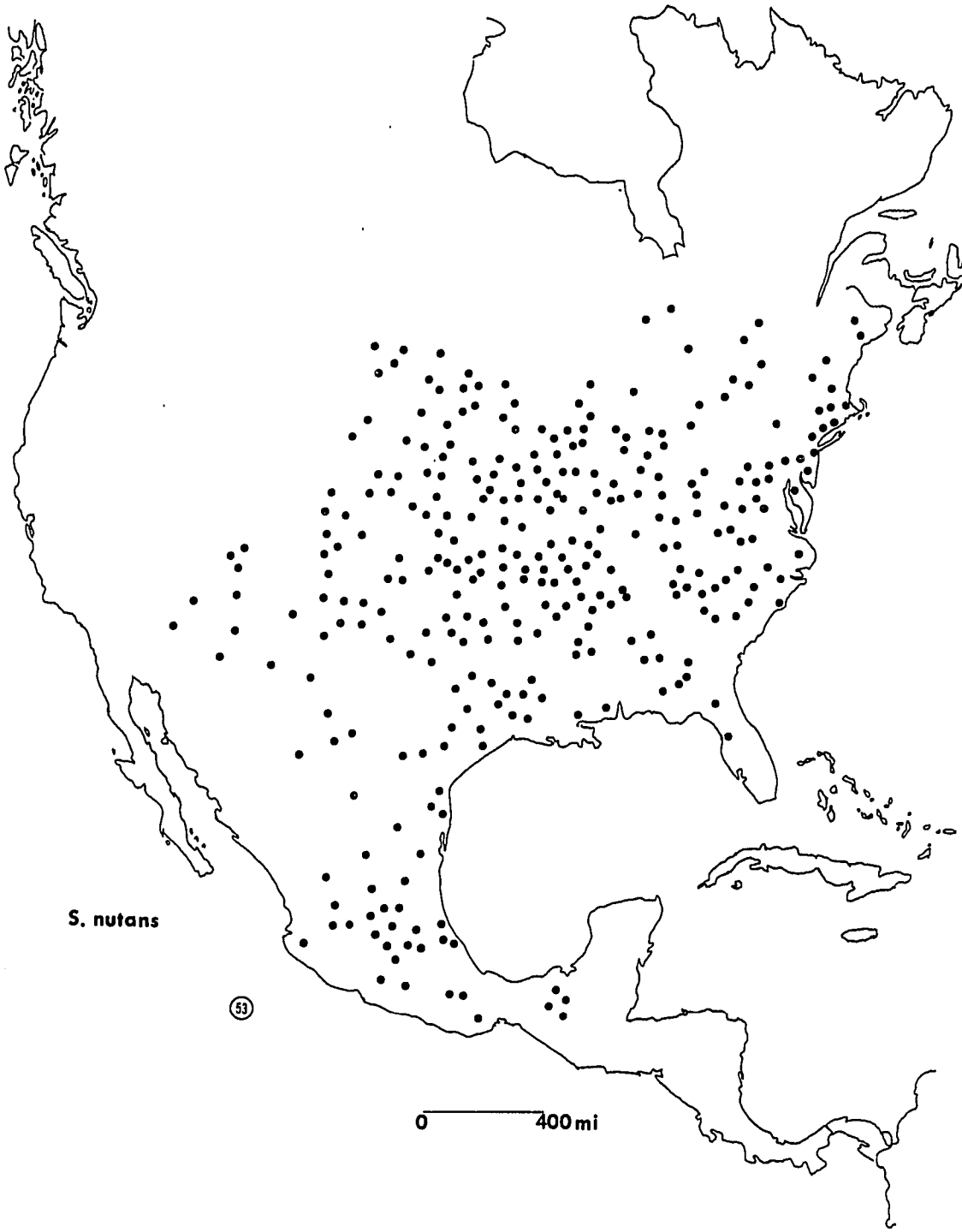
Sorghastrum nutans has a variable altitudinal range. In Canada and the U.S. it may occur from 100 m to 1500 m. In Mexico it mainly inhabits altitudes of 1000-2500 m. It is adapted to quite variable environments. In Canada and U.S. is an important element of Prairies and woods. S. nutans together with Andropogon gerardii, Spartina pectinata and Panicum virgatum comprise the four principal tall grass Prairie grasses of the central U.S. (Gould, 1968).

In Mexico and in the southermost regions of the U.S. (Arizona, New

Figure 52. Sorghastrum nutans. A. Basal part, bar=5 cm. B. Inflorescence, bar=5 cm. C. Ventral view of the spikelet, bar=1 mm


A
B
C

Figure 53. Distribution of Sorghastrum nutans


S. nutans
53
0
400 mi

Mexico, Texas), S. nutans may grow in drier places like savannas, grasslands and even scrub-like vegetation. Also, is usually present in Oak and Pine woods.

Sorghastrum nutans flowers from August to November, however, some individuals may flower in June or December. In general terms, the flowering period takes place in the autumn season.

Sorghastrum nutans is closely related to S. nudipes in North America and S. stipoides in South America. S. nutans is morphologically similar to S. nudipes. The length of their spikelets and awns are very similar. The latter is confined mainly to the "Sierra Tarahumara", in Mexico, whereas S. nutans is very widespread in Mexico, United States and southern Canada. Probably S. nudipes represents a recent evolutionary line emerging from S. nutans. On the other hand, S. nutans is also related to S. stipoides, which represents the counterpart of S. nutans in South America and is very widespread along the Andes and probably represents part of the South American stock that gave rise to the North American species.

In my opinion S. nutans represents a polymorphic species. It has a wide varieties of forms along its wide distribution range. This is probably responsible for all the synonyms of the present species. Gould (1968), and some others have pointed out the existence of various polypoids within populations of Sorghastrum nutans.

NOMENCLATURE:

Linnaeus (1753) cited the species Andropogon nutans. He mentioned two elements, the first one is from Virginia (Gron. virg. 133), the second is from Jamaica (Sloane Jam. 35. Hist. 1. p. 43. t. 14. f. 2.). Baum (1967) suggested that neither of these elements should be used as the type defining this species. Furthermore, he proposed that the correct name for the taxon should be Sorghastrum avenaceum (Michaux) Nash. Meanwhile Andropogon nutans should be considered as synonym (in part) of Stipa avenacea L. and also a synonym (in part) of Trichachne nutans (L.) Baum.

Linnaeus used the Gronovian synonym (the first element) as the sole element, in the protologue of Stipa avenacea (Sp. Pl. 78. 1753). On the other hand, the Sloane synonym was also used as a synonym for Andropogon insulare L. (Hitchcock, 1908a). This specimen is from Jamaica, where S. nutans is not present.

In the description of Stipa avenacea, the specimen mentioned is the same as the one referred to in the original description of Andropogon nutans: Virginia, Gron. virg. 133 (LINN 1211.3). On the other hand, the Sloane specimen which was used as a synonym of A. insulare (LINN 1211.20) corresponds to the genus Trichachne (=Digitaria).

In conclusion, the specimen from Virginia (LINN 1211.3) corresponds to the present species. It was verified by means of the microfiche of the Linnean specimen. This means that probably Linnaeus misidentified Stipa avenacea which really represents an Andropogon nutans sensu Linnaeus. The Sloane specimen should be rejected because it corresponds

to a different taxon. The Gronovian specimen collected by Kalm (Hitchcock, 1908b), should be the holotype and consequently the basionym of Andropogon nutans L.

Michaux (1803), proposed the new name Andropogon avenaceus, based in one of his specimens from Illinois. This name has commonly been used for the present species, however, it is shown in the prior paragraph that the legitimate name for this species should be Sorghastrum nutans.

Elliott (1816) proposed the new species Andropogon ciliatus based on a specimen from South Carolina. The description and the specimen fit quite well within the present species limits.

Rafinesque (1830) included this species within the genus Poranthera. He proposed two new combinations, Poranthera nutans and Poranthera ciliata. These names are based on Andropogon nutans and Andropogon ciliatus respectively.

Gray (1848) assigned this species to Sorghum. He suggested the new combination Sorghum nutans which is based on Andropogon nutans.

Bentham (1881) did not accept the present species within Sorghum. He proposed that it should be considered as a species of Chrysopogon. In the same publication, Notes on Gramineae, the author suggested the new combinations, Chrysopogon nutans and Chrysopogon avenaceus.

Chapman (1883) agreed with Gray's idea (including Sorghastrum species within Sorghum) and proposed the new combination Sorghum avenaceum, which is based on Andropogon avenaceus.

Hackel (1883) included many of Sorghastrum species within different

subspecies and varieties of Sorghum nutans. This author proposed for the present species the name Sorghum nutans ssp. avenaceum var. " " genuinum. Hackel's name is based on a combination of both Andropogon nutans and Andropogon avenaceus.

Based on a specimen from Mexico (Gouin 53), Fournier (1881) proposed the new species Andropogon albescens. However, this represents a synonym of the present species.

Trinius (in Fournier 1881), suggested the new species Andropogon confertus. It is based on a specimen from Texas (Berlandier 1873). This species is a synonym of Sorghastrum nutans.

Hackel (1889) did not accept Sorghum nutans. He transferred all Sorghastrum species, as subspecies and varieties of Andropogon nutans. For the present species, Hackel proposed the name Andropogon nutans var. avenaceus, which is based on both A. nutans and A. avenaceus

Taking in consideration Bentham's (1881) suggestion, Coville and Branner (1891) proposed the new combination Chrysopogon nutans var. avenaceus. This combination is based on Chrysopogon nutans and Chrysopogon avenaceus.

Nash (1901) proposed the transference of this and other species to the genus Sorghastrum He suggested the new combination Sorghastrum avenaceum. The same author, Nash (1903), suggested the new combination Sorghastrum nutans based on Andropogon nutans. It has been explained before, that this name should be considered legitimate for this species.

Lunell (1915) included the present species within the genus Chalcoelytrum. He proposed the combination Chalcoelytrum nutans which is

based in Andropogon nutans.

Finally, Beetle (1982) suggested the new combination Sorghastrum albescens which is based on Andropogon albescens, a synonym of the present species.

10. Sorghastrum pellitum (Hackel) Parodi, Rev. Fac. Agron. Vet. Univ. Buenos Aires 7(1):154. 1930. Sorghum nutans (L.) Gray ssp. pellitum Hackel, Fl. Bras. 2(3):275. 1883. Type: ARGENTINA. Mendoza, s.d., Gillies 33 (Holotype: US!; Isotype: NY!). (Figs. 54A, 54B and 54C).

Sorghum nutans (L.) Gray ssp. albescens Hackel, Fl. Bras. 2(3):275. 1883 Type: BRAZIL: Brasilia austro-orientali, s.d., Sellow s.n. (Holotype: W). Not seen.

Andropogon nutans (HBK) var. pellitus (Hackel) Hackel, DC. Monogr. Phanerog. 6:532. 1889. Based on Sorghum nutans (L.) Gray ssp. pellitum Hackel.

Andropogon nutans HBK var. albescens (Hackel) Hackel, DC. Monogr. Phanerog. 6:531. 1889. Based on Sorghum nutans (L.) Gray ssp. albescens Hackel.

Andropogon pellitus (Hackel) Herter, Est. Bol. Uru. 27. 1930. Based on Andropogon nutans HBK var. pellitus (Hackel) Hackel.

Sorghastrum flexuosum Swallen, Phytologia 14(2):96. 1966. Type: BRAZIL. SANTA CATARINA: Fazenda Ernesto Schiede, Campo Alegre, 19 Oct 1957, Reitz & Klein 5347 (Holotype: US!).

Sorghastrum nutans (L.) Nash ssp. pellitum (Hackel) Burkart. Fl. Ilus. Entre Rios 2:476. 1969. Based on Sorghum nutans (L.) Gray ssp. pellitum Hackel.

Sorghastrum nutans (L.) Nash ssp. albescens (Hackel) Burkart. Fl. Ilus. Entre Rios 2:476. 1969. Based on Sorghum nutans (L.) Gray ssp. albescens Hackel.

Rhizomes lacking. Culms erect, caespitose, 1.2-3 mm diam., 0.40-1.20 (-1.40) m tall, glabrous. Internodes terete, smooth, frequently pubescent, seldom glabrous. Leaves: blades narrow, filiform, convolute, 15-40 (-60) cm long, 1-3 (-5) mm wide, generally pilose, but sometimes glabrous, margins serrulate; ligule erect, obtuse, 1.4-4 (-5) mm long, pubescent; sheath tight, 10-25 cm long, 2-3 mm wide, generally glabrous and shining, sometimes hairy at the ligular zone. Inflorescence erect, villous, golden or yellow-brownish, frequently dense, sometimes semi-open, 15-30 (-40) cm long; rachis pubescent; peduncle 15-45 cm long, pubescent. Spikelets dorsally compressed, oblong-lanceolate, 4.5-7 mm long. Glumes coriaceous; glume I coriaceous, truncate, 4.5-6.8 mm long, 1.2-1.8 mm wide, strongly pubescent, 7-9-nerved; glume II acute, 4.5-7 mm long, 1.2-1.8 mm wide, sparsely pubescent, 5-nerved; Sterile lemma hyaline, bifid, 3.5-6 mm long, 1-1.6 mm wide, ciliate, 2-nerved. Fertile lemma hyaline, bifid, 3-6 mm long, 0.5-1.5 (-1.8) mm wide, ciliate, 3-nerved. Awn once or twice geniculate, 1-2.5 cm long, 2-4 times longer than the spikelet. Anthers 2.5-4.5 mm long. Caryopsis 2.5-3 mm long. Sterile Pedicel 3.5-7.5 mm long, strongly pubescent. Chromosome number 2n=20.

Representative specimens examined: ARGENTINA. BUENOS AIRES: Villa Arcadia, vias ferreas, 8 Dec 1970, Burkart 28147 (SI); Mar de la Plata,

25-27 Dec 1925, Clos & Molfino 259 (BAB); Pergamino, 20 Nov 1927, Parodi 8161 (US); Tandil, La Cascada, 25 Nov 1937, Troncoso 1297 (F, BAB, US); Pdo. Gral Pueyrredon,, Sierra Valdez, al E. del casco de la estancia, 18 Nov 1977, Rugolo et al. 787 (SI); Pdo. Pellegrini, 29 Nov 1940, Cabrera 6968 (NY); Pdo. Rivadia, Est. America, 2 Jan 1945, Schulz 5830 (CTES); Pdo. Tornquist, Sierra de la Ventana, Cerro de la Ventana, 17 Jan 1940, Cabrera 5779 (NY); CHACO: alrededores de Resistencia, Nov-Dec, Meyer 369 (SI); Dtto. Mayor L. J. Fontana, E. Urien, 22 Oct 1961, Schulz 11387 (CTES); Dtto. 1° de Mayo, Col. Benitez, 26 Nov 1906, Stuckert 16260 (MO); Dtto. 9 de Julio, Las Brenas, Schulz 10784 (CTES); Dtto. Tapenaga, Campo Bonazzola, Nov 1940, Rodrigo 2419 (NY); CORDOBA: Capilla del Monte, Dec 1889, Kurtz 6647 (NY); Copina, 13 Jan 1940, Burkart 10119 (MO); Dtto. Punilla, Pampa de la Ollada, 26 Nov 1969, Cuti 487 (CTES, MO); Dtto. Rio Segundo, Col. Ruiz Videla, cerca de Villa del Rosario, 12 Nov 1902, Stuckert 12034 (MO, NY, SI); Dtto. San Javier, Loma Bola, 16 Jan 1966, Hunziker 8295 (SI); Sierra grande, El Mirador, entre Rio Yuspe y Cuchilla Nevada, 2 Feb 1951, Hunziker 2714 (SI); CORRIENTES: Dtto. Bella Vista, Ruta 27, 10 km S de Bella Vista, Toropi, 13 Oct 1974, Schinini & Cristobal 9770 (CTES); Dtto. Curuzu, Cuatia, 6 Sep 1961, Pedersen 6064 (M). NY. TEX, US); Dtto. Empedrado, estancia Las Tres Marias, 7 Sep 1951, Pedersen 1175 (US); Dtto. Ituzaingo, Rapidos del Apipe, 14 Oct 1976, Quarin 3440 (CTES); Dtto. Lavalle, 1 km N de Santa Lucia, Colonia Echeverria, 25 May 1973, Schinini 6577 (CTES); Dtto. Mercedes, 8 Aug 1966, Royo 247 (CTES). Dtto. Santo Tome, Ruta 37, 5 km E de Gdor. Virasoro, 14 Nov 1974, Schinini & Carnevalli 10411 (CTES); ENTRE RIOS:

Dtto. Concordia, Salto Grande, 11 Oct 1950, Hunziker 4535 (BAB); Dtto. Federacion, estancia Buena Esperanza, 14 Feb 1964, Pedersen 7146 (NY); Parana, camino a La Toma, 2 Nov 1962, Boelcke & Correa 9234 (MO); Tizanos Pinto, 10 Oct 1980, Munoz 1458 (SI); JUJUY: Dtto. Capital, camino a Tilquiza, 22 Feb 1983, Hunziker et al. 10353 (SI); Dtto. Santa Barbara, Abra de los Morteros, 26 Jan 1975, Zuloaga & Deginani 270 (SI); Dtto. Tumbaya, 6 Apr 1971, Vercorst 8492 (CTES); LA FE: Ceres, Oct 1892, Kuntze s.n. (NY); MISIONES: Dtto. Apostoles Apostoles, 29 Nov 1943, Burkart 14264 (SI); Dtto. Candelaria, Loreto, 15 Oct 1950, Montes 15252 (SI); Dtto. San Ignacio, Campo Viena, 15 Oct 1950, Montes 10853 (US); PAMPA: General Acha, 19 Dec 1951, Ragonese & Piccinini 8257 (BAB, ENCB); medanos cerca de Gral. Acha camino a Santa Rosa, 28 Nov 1959, Troncoso 20490 (SI, US); Leventue, Trenque Lauquen, Ruta 148, 21 Dec 1963, Cano 2904 (BAB); Toay, Los Pinos, 20 Oct 1963, Cano 2817 (BAB, CTES); Utracan, ruta 148, Valle Daza, 28 Dec 1963, Cano 2973 (BAB, CTES); Victorica, 26 Dec 1920, Wetmore 836 (US); SAN LUIZ: El Rincon, Sierra de los Comechingones, 4 km E of Merlo, 29 Jan 1974, Conrad 2499 (MO); TUCUMAN: Siambon, Sierra de Tucuman, Jan 1874, Lorentz & Hieronymus 848 (ISC); Valle Calchaqui, San Jose, 24 Jan 1933, Parodi 10695 (CTES); Dtto. Burroyaco, cerro del Campo, 29 Mar 1930, Venturi 10248 (NY); Dtto. Tafi, Cerro de Taficillo, 25 Jan 1930, Venturi 10039 (MO, NY, US); Dtto. Trancas, Leocadio Paz, 15 Mar 1927, Venturi 6753 (US); SALTA: Virrey Toledo, 1 Feb 1940, Parodi 13470 (US). BRAZIL. MATO GROSSO: between Campo Grande and Dourados, 14-17 Feb 1930, Chase 10914 (US); PARANA:

Guarapuava. 20-23 Mar 1946, Swallen 8900 (US); RIO GRANDE DO SUL: Caseros, 7 Nov 1962, Rosengurtt 9051 (US); P. Alegre, 6 Nov 1948, Rambo 37865 (WIS); Pelotas, 14 Oct 1954, Costa Sacco 195 (F, NY, US); Uruaguaiana, 9 Dec 1945, Swallen 7649 (US); Vacaria, 2 Nov 1979, Flores 108 (ISC); SANTA CATARINA: Mun. Agua Doce, Fazenda Esperanza, 6 km S of Horizonte, 4 Dec. 1964, Smith & Klein 13500 (ISC); Mun. Bom Jardim, at Rio Capivari, 15 Dec 1971, Smith & Klein 15806 (US); Mun. Bom Retiro, 26 Oct 1957, Reitz & Klein 5485 (US); Mun. Campo Alegre, lower Fazenda of Ernesto Schiede, 9 Nov 1956, Smith & Klein 7490 (NY, US); Mun. Curitibanos, Campos Novos, 5 Dec 1956, Smith & Klein 8291 (NY); Mun. Lajes, Estrada da Rodagem Federal Km 37, S of Lajes, 17 Mar 1957, Smith & Klein 12243 (US); Mun. Porto Uniao, 4 Feb 1957, Smith & Klein 10771 (NY); PARAGUAY: Bernal Cue, Cordillera de Altos, Oct 1943, Pavetti & Rojas 10651 (US); between Caacupe and Tobaty, 1 Feb 1937, Archer & Rojas 4869 (US). URUGUAY: Dtto. Artigas, Sta. Rosa de Cuareim, 27 Nov, Herter 984 (MO); Dtto. Florida, Estancia Rincon de Santa Elena, picada Castro, Arroyo Mansavillagra, 28 Nov 1948, Gallinal 5939 (US); Dtto. Rocha, Maravillas, 17 Nov 1948, Herter 984c (MO); Dtto. Soriano, Mercedes, 13-18 Nov 1924, Schroeder 18064 (US).

Sorghastrum pellitum is characterized by its pubescence. This species shows a velvet-like aspect, due to the presence of hairs on both glumes, sterile pedicel, and leaves. In addition, the individuals of this species are commonly short and show narrow and convolute leaves. S. pellitum may be confused with S. viride, however the latter has a glabrous second glume and plants generally do not show a velvet-like

aspect.

Sorghastrum pellitum is distributed in South America, in Argentina, Brazil, Paraguay and Uruguay (Fig. 55). In Argentina, it occurs in the Northern and Central regions. In Brazil, Paraguay and Uruguay, S. pellitum is present in the southermost zones.

Sorghastrum pellitum is well adapted to dry zones like savannas, dry banks and hillsides. The present species is a dominant grass in the Argentinan Pampas. However, it may also grow in humid places. This species inhabits lowlands, ranging frequently from sea level to 1000 m. Occasionally, some individuals of this species may occur at 2000 m.

Sorghastrum pellitum flowers mainly from September to January, which corresponds to the Spring season for the Southern Hemisphere. This species along with S. viride are the only ones within the genus Sorghastrum that do not flower in the autumn.

Sorghastrum pellitum and Sorghastrum viride are related. Morphologically they are similar. Phenotypically both share a flowering period different from the rest of Sorghastrum species. Ecologically speaking, these species have flexible requirements, however, S. pellitum occurs principally in lowlands and dry zones, meanwhile S. viride inhabits highlands and wet areas. However, these species are partially sympatric and probably they intercross, giving rise to a hybrid population that occurs either in lowlands or highlands, as well as in dry or wet places. Hackel (1889) and Pereira (1982), have already pointed out the existence of intermediate forms belonging to the present species.

Figure 54. Sorghastrum pellitum. A. Basalpart, bar=5 cm. B. Inflorescence, bar=5 cm. C. Ventral view of the spikelet, bar=1 mm

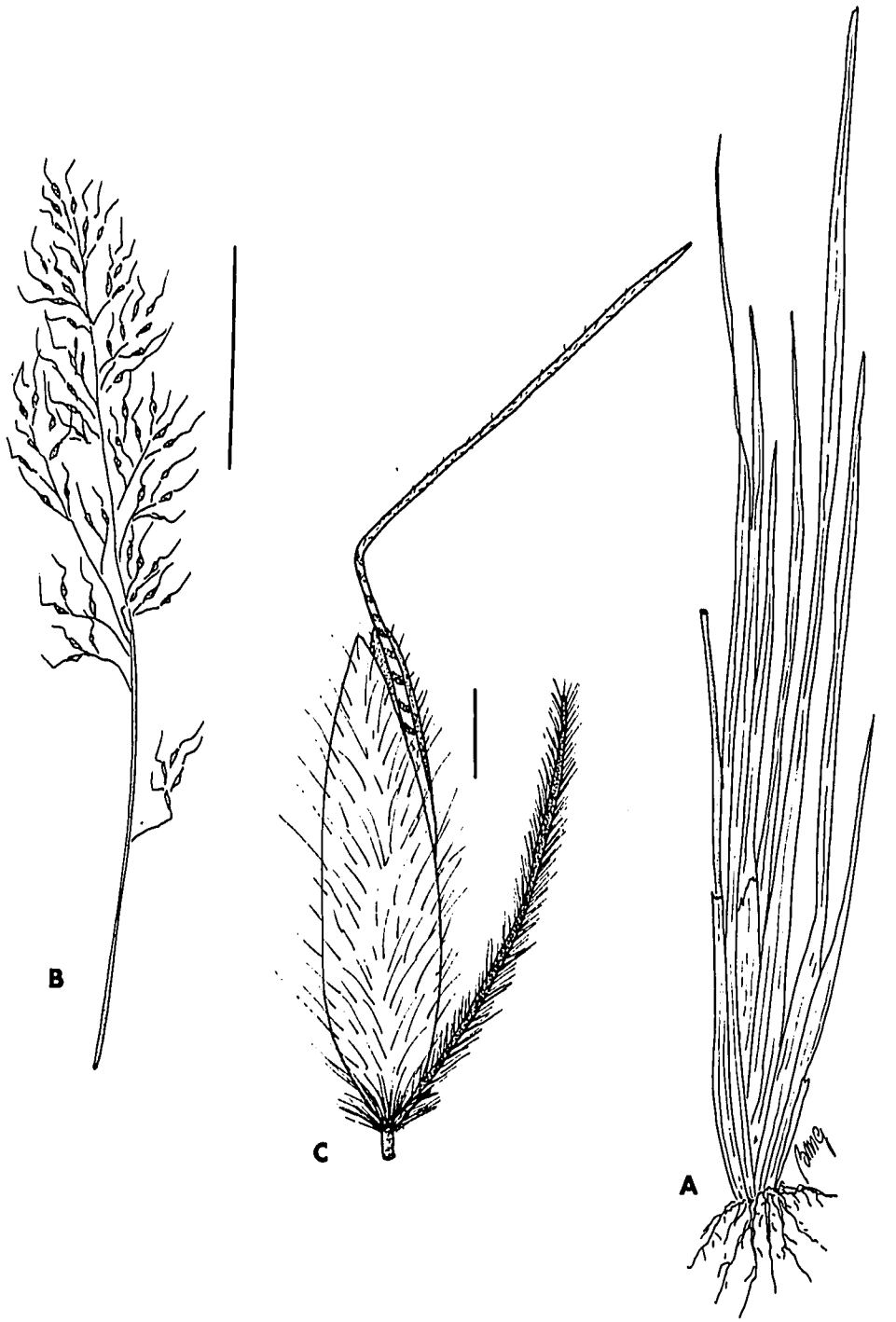

B
C
A

Figure 55. Distribution of Sorghastrum pellitum


S. pellitum
55
0
600mi

In fact, I think that the divergence in opinions about the taxonomic status of S. pellitum and S. albescens is due to this hybridization. Due to the fact that there is no other information available to confirm or reject this speculation, the species Sorghastrum pellitum may include all those individuals showing both glumes pubescent. On the other hand Sorghastrum viride has a glabrous second glume.

NOMENCLATURE:

Hackel (1883) included most of Sorghastrum species as subspecies of Sorghum nutans. He proposed for the present species, the name Sorghum nutans ssp. pellitum. It is based on a specimen from Mendoza, Argentina (Gilles 33). In the same publication, Flora Brasiliensis, Hackel also cited Sorghum nutans var. albescens as a subspecies from Brazil that shows as a different characters from S. pellitum, pubescent sheaths and a glabrous second glume.

In 1889, Hackel transferred all Sorghastrum species to different varieties of Andropogon nutans. The present species was proposed as A. nutans var. pellitus. In this publication, Hackel mentioned the presence of many different forms within the present species. In addition, he suggested A. nutans var. albescens differed from variety pellitum only in the lack of a pubescent second glume. I think that variety albescens represents a hybrid population with many different forms. This hybrid probably originated between Sorghastrum pellitum and Sorghastrum viride. The distinctive characters mentioned by Hackel for the variety albescens (pubescent sheaths and glabrous second glume) are shown by some individuals, however some others have pubescent sheaths and a second

glume pilose, or within spikelets of the same inflorescence, some show different degrees of pilosity, and others are strictly glabrous.

Herter (1930), did not accept the species Andropogon nutans proposed by Hackel and consequently suggested the name Andropogon pellitus.

Parodi (1930), based on Nash's (1901) transference of this species, as well as others, to the genus Sorghastrum, suggested the new combination Sorghastrum pellitum. This should be considered the legitimate name for the present species. This name is based on the basionym Sorghum nutans (L.) Gray ssp. pellitum Hackel. Consequently, the type specimen should be that from Mendoza, Argentina (Gilles 33).

In 1966 Swallen proposed the new species Sorghastrum flexuosum, which is based on a specimen from Santa Catarina, Brazil (Reitz & Klein 5347). However, both the specimen and the description fit with the present species.

Burkart and Toursarkissian (1969) suggested that in Sorghastrum nutans there were two subspecies: S. nutans ssp. albescens and S. nutans ssp. pellitum. However, I think that S. pellitum has enough distinctive characters to be considered a separate species, and that the subspecies albescens represent all those "forms" already mentioned.

Finally, Pereira (1982) proposed the new combination Sorghastrum albescens. The author pointed out that the only difference between the proposed species and S. pellitum is that S. albescens has very short hairs in the glumes. In S. pellitum the glumes have long, hirsute pubescence. Until further information is available it is adequate to

include S. albescens as a synonym of S. pellitum.

11. Sorghastrum rigidifolium (Stapf) Chippindall, in Evans, roadside observations on the vegetation of East and Central Africa. Bot. Survey Memoir 22: 247. 1948. Sorghum rigidifolium Stapf, Flora of Tropical Africa 9:141. 1919. Type: UGANDA. Nandi, Sibu, s.d., James s.n. (Holotype: K?). Not seen. (Figs. 56A, 56B and 56C).

Miscanthidium fuscescens Pilger, Notizabl. Bot. Gart. Berlin 11:806. 1933. Type: TANZANIA. Issovi, 1931, Schlieben 1010 (Holotype: K!).

Sorghastrum trollii Pilger, Notiz. Bot. Gart. Berlin 14:95. 1938. Type: TANZANIA. IRINGA: Iringa-Dabaga, Mar 1934, Troll 5268 (Holotype: K). Not seen.

Sorghastrum rigidifolium Swallen, Phytologia 14(2):97. 1966. Type: CUBA. Herradura, Pinar del Rio, 7 Sep 1920, Ekman 11603 (Holotype: US!).

Sorghastrum fuscescens (Pilger) Clayton. Kew Bull. 30(3):509. 1975. Based on Miscanthidium fuscescens Pilger.

Rizome lacking. Culms stout, erect (1.5-) 2.5-4 mm diam., 1-2 m tall, smooth. Internodes terete, smooth, glabrous or slightly pubescent below the nodes. Leaves: blades flat or slightly involute, 25-40(-55) cm long, 1-5(-8) mm wide, glabrous or slightly scabrous, apex acute, margins serrulate; ligule short, 1.5-3 (-4) mm long, slightly pubescent; sheaths the uppermost very long, 15-40 cm ong, 2-6 mm wide, smooth, glabrous or pubescent close to the nodes. Inflorescence linear-oblong, erect, seldom slightly nodding, 20-35 (-45) cm long; rachis smooth,

glabrous; peduncle 20-50 (-60) cm long, glabrous. Spikelets dorsally compressed, lanceolate, dark, 4.5-6.5 mm long; callus blunt,villous. Glumes coriaceous; glume I truncate, 4.5-6 mm long, 1-1.6 (2) mm wide, pubescent, 7-9-nerved; glume II acute, 4.5-6(-7) mm long, 1-1.4 (2) mm wide, glabrous, 5-nerved. Sterile lemma lanceolate-oblong, hyaline, bifid, 4-5.5 (6) mm long, 1-1.6 mm wide, ciliate, 2-nerved. Fertile lemma oblong, hyaline, bifid,3-5.5 mm long, 0.5-1.2 mm wide, ciliate, 3-nerved. Awn once or twice geniculate, 1.5-3 cm long, 3-5 times longer than the spikelet. Anthers 3-4 mm long. Caryopsis 1.5-3.5 (-4.5) mm long. Sterile Pedicel 3-5 cm long, pubescent. Chromosome number 2n=40, 60.

Specimens examined: BURUNDI. Ruyigi, Gihofi Moso, 31 Jan 1976, Reekmans 4758 (MO); BURURI: Bukemba-Muzye, 12 May 1981, Reekmans 10218 (MO). CONGO. Kiofi-Mosso-Urundi, 18 Dec 1951, Reed 943 (MO); Kyotera-Masaka, 14 Jun 1971, Katende 1006 (MO). CUBA. 1865, Wright 3896 (NY); PINAR DEL RIO: palm-barrens, W of Guane, 21-22 Nov 1911, Shafer 10353 (MO, US); Mangas, at Pueblo Nuevo, 9 Oct 1923, Ekman 17592 (US); Santa Cruz de los Pinos, savannas at Finca Mamey, 17 Oct 1923, Ekman s.n. (LL, F. MO, NY, US). ETHIOPIA. about 60 km SW of Jimma, along road to Bonga, 4 Jun 1965, Wilde et al. 6976 (MO). KENYA. Kitale grass nursery, 15 Jan 1959, Heady 1471 (MO); KAKAMEGA: Kakamega Forest, near Forest House, 8 Mar 1972, Backeus & Johnson 361 (MO). NAIROBI: Mambasasa, Utwani, 18 Oct 1957, Greenway & Rawlines 9376 (US); Nairobi National Park, 28 May 1974, Mburi 449 (MO). MALAWII. NYASALAND: Namwevas, 8 May 1950, Wielhe

570 (MO); Nuposa, Wambo, 13 May 1952, Jackson 814 (MO). MALI. Bamako, Sotuba, 30 Sep 1958, Adam 15349 (MO). RHODESIA. Kalambo River, Abercorn, 7 May 1961, Vesey & Fitzgerald 3383 (MO); Kasaushi Dambo, 55 km ESE of Mporokoso, 13 May 1962, Robinson 5180 (B); near Muzombwe, western side of Mweru-wa-ntipa, 15 Apr, 1961, Vesey & Fitzgerald 3218 (MO). SENEGAL. Tambacounda, Niokolo-Koba, 20 Oct 1958, Adam 15652 (MO); Matam, 29 Oct 1938, Jacques & Georges 27956 (MO). SOUTH AFRICA. Durban, Wentworth, s.d., Ward 6095 (MO); Enseleni Nature Reserve, s.d., Smook 1887 (MO). TANZANIA. Agula, Mbuga, s.d., Shaboni s.n. (US); IRINGA: Mufindi, 8 May 1968, Renvoize & Abdallah 2026 (US); NJOMBE: Njombe-Songia Rd., 28 Feb 1963, Richards 17686 (MO); RUNGWE: Lusungu and Ipindi Rivers, 22 May 1957, Richard 9888 (NY, US); TUNDURU: Litungura, about 6.5 jm E of The Songea District Boundary, 6 Jun 1956, Milne, Redhead & Taylor 10596 (US). UGANDA. Soroti, s.d., Stephens S.14 (MO). UPPER VOLTA. 20 km ESE of Boromo, 29 Aug 1973, Sihvonen 176 (MO).

Sorghastrum rigidifolium is distinguished by its erect panicle, with a linear-oblong shape, as well as by the glabrous sheaths, and the long and well developed awns. It may be easily confused with Sorghastrum trichopus, with whom it is partially sympatric. However, the latter has usually an open and loose panicle and small and straight awns; whereas the present species usually shows a linear-oblong inflorescence and well developed awns.

Sorghastrum rigidifolium is distributed in Africa, from the Central-West region, in Senegal, through Mali, Upper Volta and Nigeria (Fig. 57). It occurs down to The African Democratic Republic and Ethiopia, until

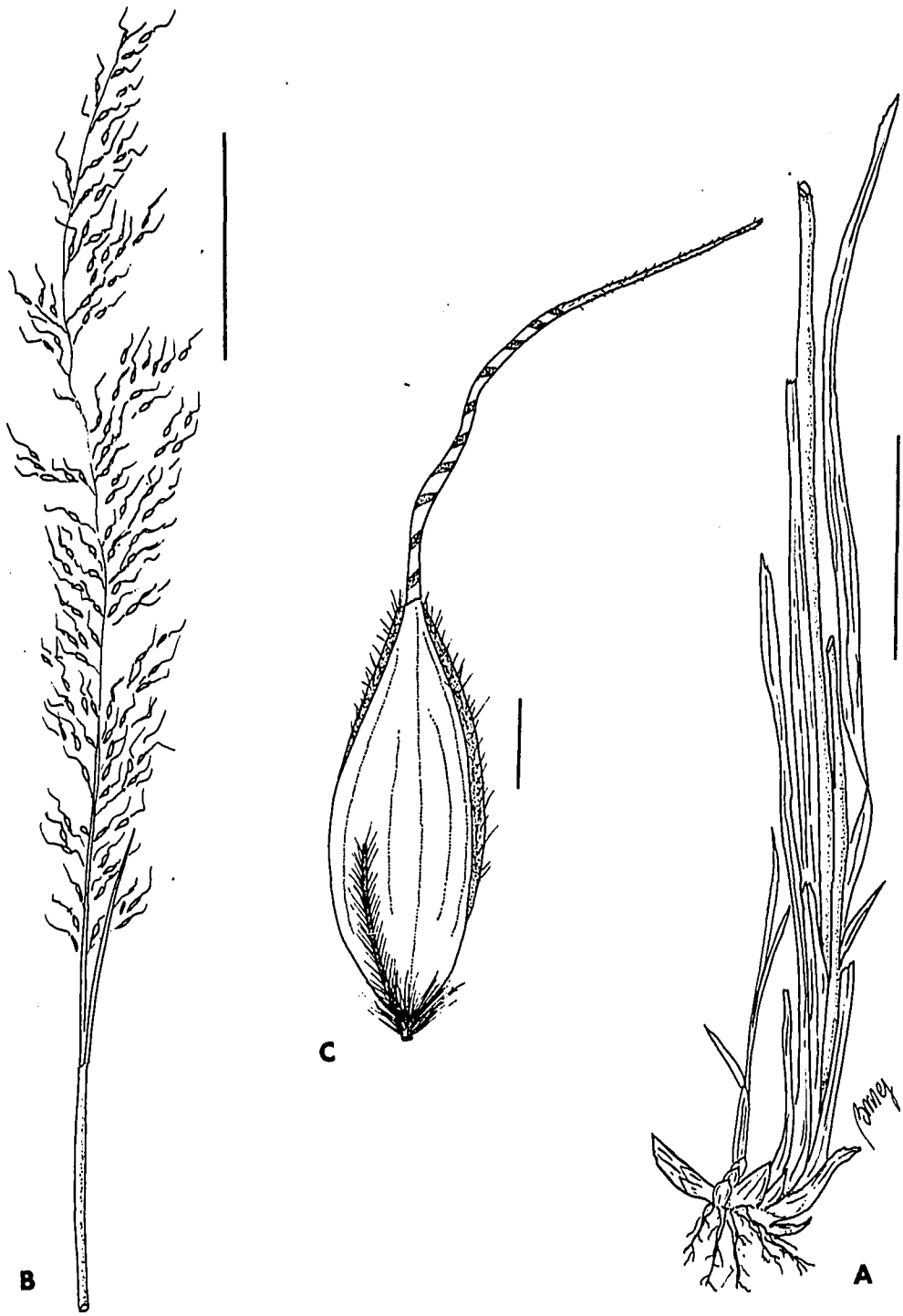
South Africa. This species is well adapted to medium and high altitudes, and its distribution pattern seems to follow some principal mountain chains, such as Kenya and Ethiopia Highlands, the "Chaine des Monogos" in Northern Congo, the "Bauchi Plateau, in Nigeria, etc.

In addition this species has also been found inhabiting Cuba. The similarities in morphology, leaf cross anatomy and epidermal features support the fact that is the same species. Because this species is distributed in a normal pattern in Africa, following the mountain chains; I think that its presence in Cuba is due to introduction. All the Cuban specimens that were observed, occurred in the same locality, a farm in Pinar del Rio. Usually in these old farms many "new species" were brought from other parts of the world as a way of improving pastures. In summary, I speculate that the present species originated in Africa and was brought to Cuba.

Sorghastrum rigidifolium is well adapted to sandy woodlands, and sometimes to swampy or boggy areas. Occasionally, it may occur on savannas of heavy soils. The altitudinal range of the present species varies from 900-3000 m. It flowers during the months of August to November in the Northern Hemisphere and from February to May in the Southern Hemisphere. In both cases this corresponds to the autumn season.

Sorghastrum rigidifolium is related to Sorghastrum minarum. Even though morphologically these two species are not very similar, both share the important anatomical character, midrib simple (formed by just one

Figure 56. Sorghastrum rigidifolium. A. Basal part, bar=5 cm. B. Inflorescence, bar=5cm. C. Ventral view of the spikelet, bar=1 mm


B
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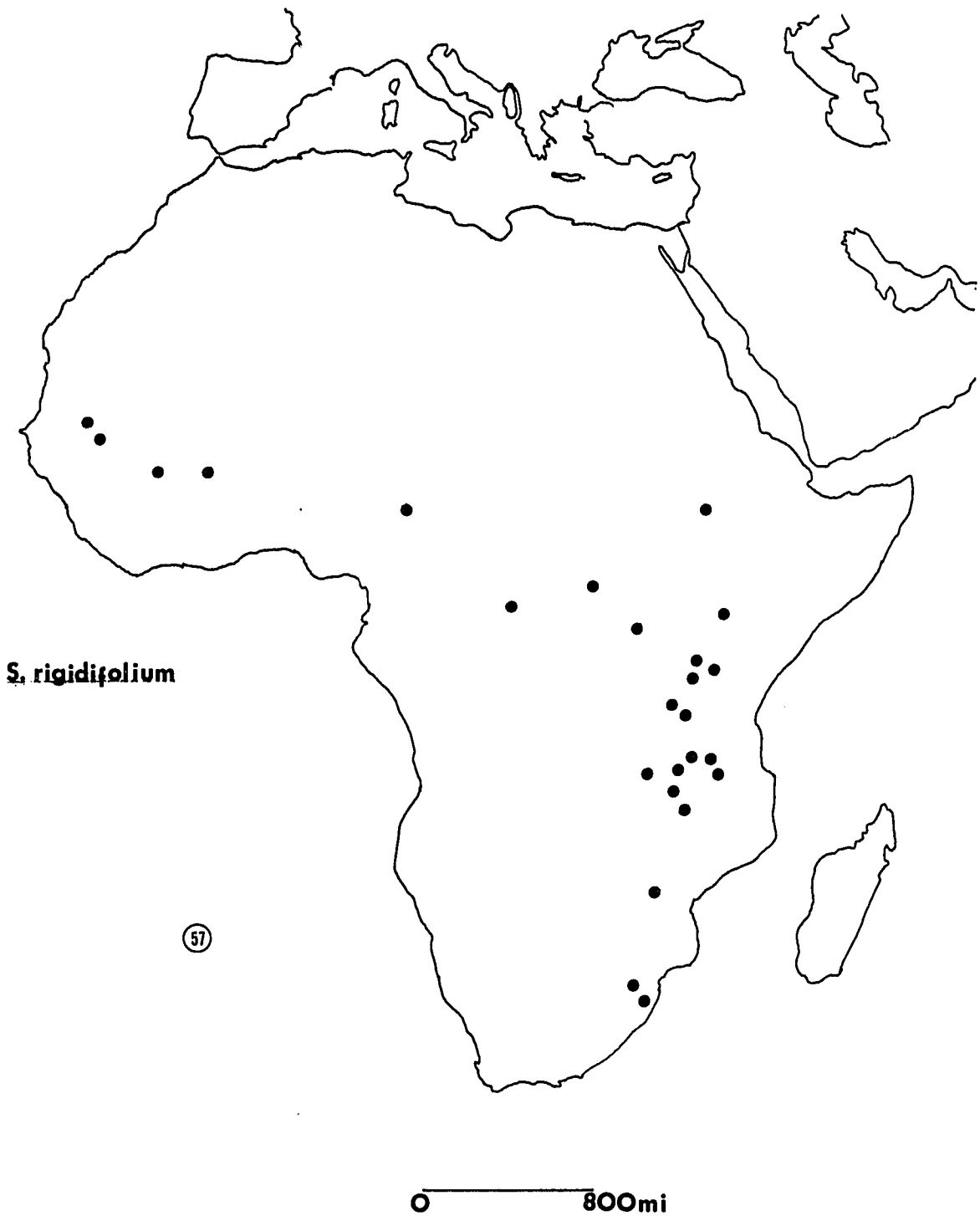
A

Figure 57. Distribution of Sorghastrum rigidifolium


S. rigidifolium
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first order vascular bundle).

Sorghastrum rigidifolium and Sorghastrum minarum stocks seem the best candidates for representing the connecting species between Africa and America. Both, in their own continents are considered the most primitive species within the genus.

NOMENCLATURE:

Stapf (1919) based on a specimen from Uganda (James s.n.). Proposed the species Sorghum rigidifolium. Even though this specimen has not been located the description by Stapf coincides with the present species.

Pilger (1933) published the species Miscanthidium fuscescens. However, the description and the type specimen from Tanzania (Schlieben 1010) fits within the limits of the present species. I think that he confused the genera Miscanthidium (with a tough rachis and both spikelets pedicelled) and Sorghastrum (with a fragile rachis, one sessile spikelet and usually a barren pedicel).

The same author, Pilger (1938) suggested the new species Sorghastrum trollii, based on another specimen from Tanzania (Troll 5268). This specimen, as well as the description fit within the limits of the present species.

Chippindall (1948) suggested the new combination Sorghastrum rigidifolium. This name is based on Sorghum rigidifolium, proposed by Stapf in 1917. This should be considered the legitimate name. Consequently the type specimen should be the one from Tanzania (James s.n.) cited by Stapf.

Swallen (1966) proposed the same name Sorghastrum rigidifolium (it

was published as a new species) for the population of the present species inhabiting Cuba. There are two reasons for the rejection of this name. First, the description and the type specimen mentioned by Swallen fit into the present species. Secondly, the author chose the same specific epithet cited before by Stapf. This means that independently of the nomenclatural status of the present species, Swallen's name should be rejected as superfluous.

Finally, Clayton (1975) proposed the new combination Sorghastrum fuscescens, based on Miscanthidium fuscescens. However, as was mentioned before, the latter should be considered synonym of the legitimate name Sorghastrum rigidifolium. Consequently, Sorghastrum fuscescens is also a synonym of this species.

12. Sorghastrum scaberrimum (Nees) Herter, Rev. Sud. Bot. 6: 136. 1940. Trachypogon scaberrimum Nees, Agrost. Bras. 354. 1829. Type: BRAZIL. MINAS GERAES: 1845, Widgren 927 (Neotype: US!). (Figs. 58A, 58B and 58C).

Andropogon scaberrimus (Nees) Kunth, Enum. Pl. Gram. 1:504. 1833. No type specimen cited.

Sorghum nutans (L.) Gray ssp. scaberrimum (Nees) Hackel, Fl. Bras. 2(3):275. 1883. Type: BRAZIL. MINAS GERAES: 1845, Widgren 927 (US!).

Andropogon nutans L. var. scaberrimus (Nees) Hackel, DC. Monogr. Phan. 6:532. 1889. Based on Trachypogon scaberrimum Nees.

Rhizome lacking. Culms erect, simple, caespitose, (1-) 2-3.8 mm

diam., 0.70-1.8 (-2.20) m tall. Internodes terete, smooth and glabrous. Leaves: blades linear, inrolled or flat, 10-40 cm long, 3-9 mm wide, often scabrous, sometimes pubescent at both surfaces or just in the abaxial face, margins serrulate; ligule subcoriaceous, truncate, 15-35 mm long; sheaths usually scabrous at the upper part, sometimes smooth, 19-30 (-40) cm long, 1-5 mm wide, seldom pubescent close to the ligular area. Inflorescence a semi-open or open panicle, 15-37 cm long; rachis terete, glabrous; peduncle (15-) 30-60 (-75) cm long, glabrous. Spikelets lanceolate, dorsally compressed, dark, 3.8-5 mm long; callus blunt, villous. Glumes chartaceous-coriaceous; glume I truncate, (3.4-) 4-5 mm long, 1-1.5 mm wide, pubescent, usually 7-9-nerved; glume II lanceolate, acute, (3.6-) 4-5.5 mm long, 1-1.5 mm wide, glabrous, 5-nerved. Sterile lemma hyaline, bifid, 3-4.5 mm long, 0.5-1 mm wide, ciliate, 2-nerved. Fetile lemma hyaline, bifid, 2.5-4 mm long, 0.5-1 mm wide, ciliate, 3-nerved. Awn once or twice geniculate, 1.3-2.2 cm long, 4 times or more longer than the spikelet. Anthers 2-3 mm long. Caryopsis 1-2 mm long. Sterile Pedicel 2.5-4 mm long, pubescent. Chromosome number 2n=20. Specimens examined: BRAZIL. s.d., Riedel s.n. (MO); Est. do Rio Itatiaia, Itatinga, planalto, Mar 1937, Brade 15627 (F, MO); MINAS GERAES: 24 Feb 1846, Regnell 1390 (US, W); Lavras, 10 Mar 1925, Chase 8824 (F, MO, NY, US); PARANA: Balsa Nova, Serra de Sao Luiz by the Rodovia de Cafe, 14 Jan 1965, Smith et al. 14417 (US); Curitiba, 20 Feb 1904, Dusen 3826 (US); Itaperucu. Mun. de Rio Branco do Sul, 14 Feb 1967, Dobrowski 2463 (CTES); Ponta Grossa, Faz Cambijan, 13 Feb 1949, Brade 19636 (US); Ponta Grossa, Lagoa Dourada, 13 Abr 1978, Dombrowski 9595

(ISC); Ponta Grossa, Vila Velha, 10 Feb 1960, Pereira 5282 (US); Tibagi, Fda. Mte. Alegre, Harmonia, 20 Feb 1953, Ghatschbach 3034 (US); SANTA CATARINA: Santa Cecilia, 11 Feb 1975, Smith & Klein 16073 (US); serra da Boa Vista, Sao Jose, 2 mar 1961, Reitz & Klein 10794 (NY, US); SAO PAULO: Campos do Jordao, Serra Mantiqueira, 20-22 May 1925, Chase 9841 (F, MO, NY, US).

Sorghastrum scaberrimum is characterized by a rigid, semi-open panicle, the spikelets having a very dark color. Usually, the individuals of this species have scabrous blades, as well as in the upper part of the sheath. S. scaberrimum may be confused with S. stipoides, however, the latter has paler spikelets and frequently shows pubescent leaves and sheaths. Furthermore, S. scaberrimum inhabits elevations ranging from 1000-2500 m, whereas S. stipoides inhabits places mostly below 1000 m.

Sorghastrum scaberrimum is distributed in the south-southeastern region of Brazil, in the states of Minas Geraes, Parana, Santa Catarina and Sao Paulo (Fig. 59). This zone corresponds to the Brazilian Highlands, including the "Serra do Mantiqueira", "Serra do Espinhaco" and the "Serra do Mar". Apparently, the present species is confined to the Brazilian Highlands and does not extend to the lower areas.

Sorghastrum scaberrimum inhabits the so called "Planaltos". It grows in sandy and argillaceous soils. It flowers from February to May, which represents the end of the summer and the beginning of the autumn for the Southern Hemisphere.

Sorghastrum scaberrimum is closely related to Sorghastrum stipoides; in general terms their morphological and anatomical characteristics are very similar. However, they can be differentiated by means of characteristics of their spikelets and inflorescence shape. The spikelets in S. scaberrimum are usually very dark whereas in S. stipoides are paler. In addition, the inflorescence in S. scaberrimum is semi-open or open, and with a rigid aspect, meanwhile in S. stipoides the inflorescence is open, loose and not rigid. Finally, S. stipoides inhabits places mostly below 1000 m, that are always associated to the Andean Mountains. On the other hand, S. scaberrimum is located mainly above 1000 m, up to 2500 m in the Brazilian Highlands.

NOMENCLATURE:

Nees (1829) included the present species within the limits of Trachypogon sensu lato. He suggested the name Trachypogon scaberrimus for the species, characterized by having scabrous leaves. No specimen was cited, however Nees also mentioned that this species was located in Brazil, Minarum province, between Villa Rica and Tejuco.

Kunth (1833) included the present species within Andropogon. He suggested the new combination Andropogon scaberrimus based on Trachypogon scaberrimus Nees. Again, no specimen was cited.

In the same year, 1883, Hackel included most of Sorghastrum species as subspecies and varieties of Sorghum nutans. He proposed Sorghum nutans ssp. scaberrimum with two varieties, " " neesianum and " " elongatum. The shape and length of the awn are the differentiating

Figure 58. Sorghastrum scaberrimum. A. Basal part, bar=5 cm. B. Inflorescence, bar=5 cm. C. Ventral view of the spikelet, bar=1 mm

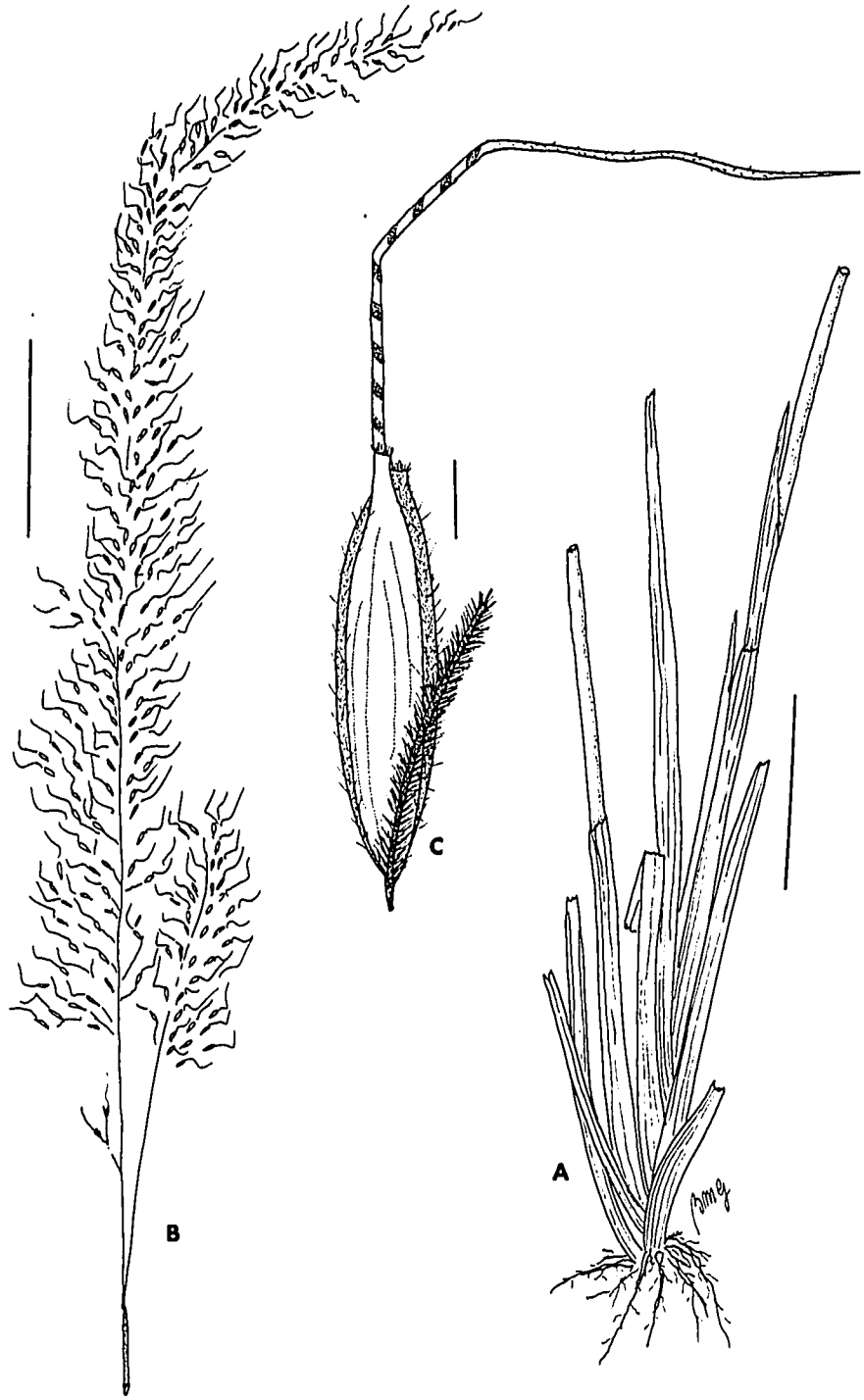
B
C
A

Figure 59. Distribution of Sorghastrum scaberrimum


S. scaberrimum
59
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600mi

characters of the varieties. However, Hackel's species, including both varieties, fit within Nees' Trachypogon scaberrimum. Consequently, it should be considered a synonym of the present species.

Hackel is the first author who cited some specimens. The specimen from Minas Geraes (Widgren 927) deposited in (US), is considered the Neotype specimen of Sorghastrum scaberrimum.

In 1889, the same author transferred all Sorghastrum species to Andropogon. He suggested the new combination Andropogon nutans var. scaberrimus with three subvarieties (neesii, elongatus and fulginosus). The differences pointed out among these three varieties are awn length, spikelet color, and location of the geniculation. However, I think that these differences constantly overlap among the individuals of the present species and cannot be applied specifically to one variety.

Once the genus Sorghastrum was accepted, Herter (1940) suggested the combination Sorghastrum scaberrimum based on Trachypogon scaberrimus Nees. This is the legitimate name for the present species.

13. Sorghastrum secundum (Elliott) Nash, Fl. SE. U.S. 67. 1903. Andropogon secundus Elliott, Bot. South Carolina and Georgia 1:580. 1816. Type: UNITED STATES. FLORIDA: dry, sandy soil, near Jacksonville, Oct, Curtiss 3644 (Neotype: US 740694!; Isoneotypes: US 740696!; US 740698!; NY!; F 148757!; F 308697!). (Figs. 60A, 60B and 60C).

Chrysopogon secundus (Elliott) Vasey, Grasses U.S. 20. 1883. Based on Andropogon secundus Elliott. No type specimen cited.

Sorghum secundum (Elliott) Chapman, Fl. SE U.S. 583. 1883. Based

on Andropogon secundus Elliott. No type specimen cited.

Andropogon unilateralis Hackel, DC Monog. Phan. 6:533. 1889. Type: UNITED STATES. FLORIDA: dry, sandy soil, near Jacksonville, Oct, Curtiss 3644 (Lectotype: US 740694!).

Rhizome lacking. Culms erect, simple, 1.5-3 mm diam., 0.90-1.50 (-1.80) m tall. Internodes terete, smooth, glabrous, or slightly pubescent below the nodes. Leaves: blades flat or involute, narrow, 20-50 cm long, (1.8-) 3-6 mm wide, apex acute, scabrous particularly on the abaxial face, margins serrulate; ligule 2.5-4 (-5.7) mm long; sheaths 20-45 cm long, 2-4.5 mm wide, generally glabrous, but occasionally pubescent in young specimens. Inflorescence a loose and open panicle, the branches erect or nearly so, all spikelets arranged on one side of the inflorescence, 15-40 cm long; rachis terete, glabrous; peduncle 25-50 (-55) cm long, glabrous. Spikelets dorsally compressed, lanceolate, dark brown to golden-brown at maturity, 6-8 mm long; callus 1-1.2 mm long, densely bearded. Glumes coriaceous; glume I truncate, 6-7.5 mm long, 1.4-1.6 (-1.8) mm wide, pubescent, 7-9-nerved; glume II linear-oblong, acuminate, 6.5-7.5 (-8) mm long, 1.3-1.6 mm wide, glabrous, 5-nerved. Sterile lemma bifid, hyaline, 4-5.5 (-6.5) mm long, 0.9-1.5 (-1.8) mm wide, ciliate, 2-nerved. Fertile lemma bifid, hyaline, 4-5.5 (-3.5) mm long, 0.6-1 (-1.2) mm wide. Awn twice-geniculate, dark brown, 3-4 cm long, 4-6 times longer than the spikelet. Anthers 2.5-4.5 mm long. Caryopsis reddish, 2-3 mm long. Sterile Pedicel 4-6 (-7.6), pubescent. Chromosome number 2n=20.

Representative specimens examined: UNITED STATES. ALABAMA: Stapleton, 24 Sep 1939, Silveus 5145 (LL, TEX); FLORIDA: Apalachicola, s.d., Chapman s.n. (NY); Bradenton, 1 Oct 1900, Tracy 7097 (F, NY, US); Branchton, 7 Oct 1930, Blanton 6801 (F); Cujoe Key, 10 Feb 1935, Swallen 5166 (US); De Funiak Springs, 27 Sep 1900, Biltmore 4642a (US); De Funiak Springs, Sep 1913, Stevens s.n. (US); W of Miami, 7 Sep 1907, Chase 3871 (ISC, US); near Jacksonville, 11 Oct 1893, Curtiss 4019 (NY); in tropical pineland, Miami, 12 Oct 1933, Duckett 214 (NY); Micanopy junction, 8 Oct 1940, Silveus 6516 (TEX); New River, 26 Dec 1895, Hitchcock 2358 (US); Orange City, enterprise junct., 10 Sep 1913, Hood 8 (US); Orange City, 22 Sep 1913, Hood 15 (US); Paradise, 27 Dec 1908, Clos 170 (US); Pasadena, St. Petersb., 15 Oct 1932, Reeves & Miller 25 (F); Pine Key, s.d., Blodgett s.n. (NY); St. Petersburg, 28 Abr 1939, Silveus 5211 (TEX); St. Vincent Island, 30 Oct 1910, McAtee 1742 (US); near Tallahassee, s.d., Berg s.n. (NY); Tampa, Oct 1877, Garber s.n. (F, NY, US); Brevard Co., Ockuchobee region, 22 Aug 1903, Fredholm 5972 (NY, US); Clay Co., Penny Farms, 15 Nov 1938, Swallen 5593 (US); Dade Co., Everglades National Park, Gate 1, Long Pine Key, 15 Aug 1961, Craighead s.n. (NY); De Soto Co., Arcadia, 19 Oct 1920, Thompson 29 (US); Duval Co., Oct 1876, Curtiss s.n. (ISC); Highlands Co., 10 miles S of Lake Placid, 5 Nov 1945, Brass 15646 (US); Lake Co., vicinity of Eustis, May 1984, Nash 753 (NY); Monroe Co., Big Pine Key, 5 Nov 1950, Killip 40661 (US); Lee Co., vicinity of Fort Myers, 18 Oct 1916, Standley 364 (F, NY); Okaloosa Co., 4.5 miles W of Mary Esther, 18 Sep 1975, Hausen & Hausen 3739 (LL); Orange Co., 8 Aug 1902, Fredholm 5459 (NY, US); Orange Co., Clarcona, 3 Nov 1899, Meislahn

104 (ISC, US); Polk Co., Bartow, 28 Sep 1898, Combs 1193 (US); Seminole Co., 8 Aug 1936, Correll 6354 (US); Volusia Co., near Tomaka Farms Settlement, 4 Oct 1981, Correll & Correll 52757 (NY); Wakula Co., between Spring Hill and Crawfordville, 30 Sep 1964, Godfrey 64654 (ISC); Walton Co., at Mossy Head, W of De Funiak Springs, 23 Sep 1956, Godfrey & Kral 55138 (NY); GEORGIA; Coffee Co., 3 miles W of Douglas, 25 Sep 1900, Harper 719 (NY); Long Co., 6 miles SW of Ludowici, 14 Sep 1974, Duncan 7869 (NY); Mcintosh Co., on W side of Sapelo Island, about 2.3 miles W of south tip of Blackbeard Island, 17 Oct 1956, Duncan 20663 (F, ISC, TEX); SOUTH CAROLINA: Aiken, Sep, Ravenel s.n. (NY); Aiken, 24 Sep 1866, Ravenel s.n. (NY); Aiken, Oct 1884, Ravenel s.n. (NY); Barnwell Co., Savannah River Operations Area of the Atomic Energy Commission, 27 Oct 1953, Batson & Kelley s.n. (US); Jasper Co., Tillman ridge, 7.4 miles NW of Tillman on Co. Rt. 119, 24 Sep 1969, Leonard & Radford 2764 (ISC, LL, NY, TEX).

Sorghastrum secundum is characterized by the presence of a unilateral inflorescence. The primary branches of the inflorescence are pointing upwards, whereas the secondary branches are pointing downwards, so that the spikelets are patent or nodding. S. secundum is similar to Sorghastrum elliotti, but the latter has smaller inflorescences, which do not present a unilateral inflorescence. Also, in many cases S. elliottii has smaller spikelets and stamens than S. secundum.

Sorghastrum secundum occurs in the southeastern region of the United States, in the states of Florida, Georgia, Alabama and South Carolina

(Fig. 61). This region represents the southern limits of the Appalachian Mountains. S. secundum does not extend to northern and western areas, probably due to the Appalachian Mountains that act as natural barriers. This species grows in lowlands up to 1000 m, however is always associated to the southeastern Appalachian lower zones.

Sorghastrum secundum especially inhabits woodlands and areas with sandy soils, or sometimes occurs close to marshy edges. It flowers in autumn, principally in the months of September and October. However, many individuals may flower in August.

Sorghastrum secundum is closely related to S. elliottii. Morphologically, both species are very similar. S. secundum and S. elliottii have similar environmental requirements. However, important anatomical differences, as well as different types of inflorescences support the existence of both species. The distribution pattern of these two species is partially allopatric. S. secundum inhabits the southestern limits of the Appalachian mountains. On the other hand, S. elliottii occurs in all the Gulf States, in many of the East Coast states, as well as all across the Sierra Madre Oriental in Mexico. Probably the Appalachian formation has been an effective barrier for the further geographic spreading of S. secundum.

NOMENCLATURE:

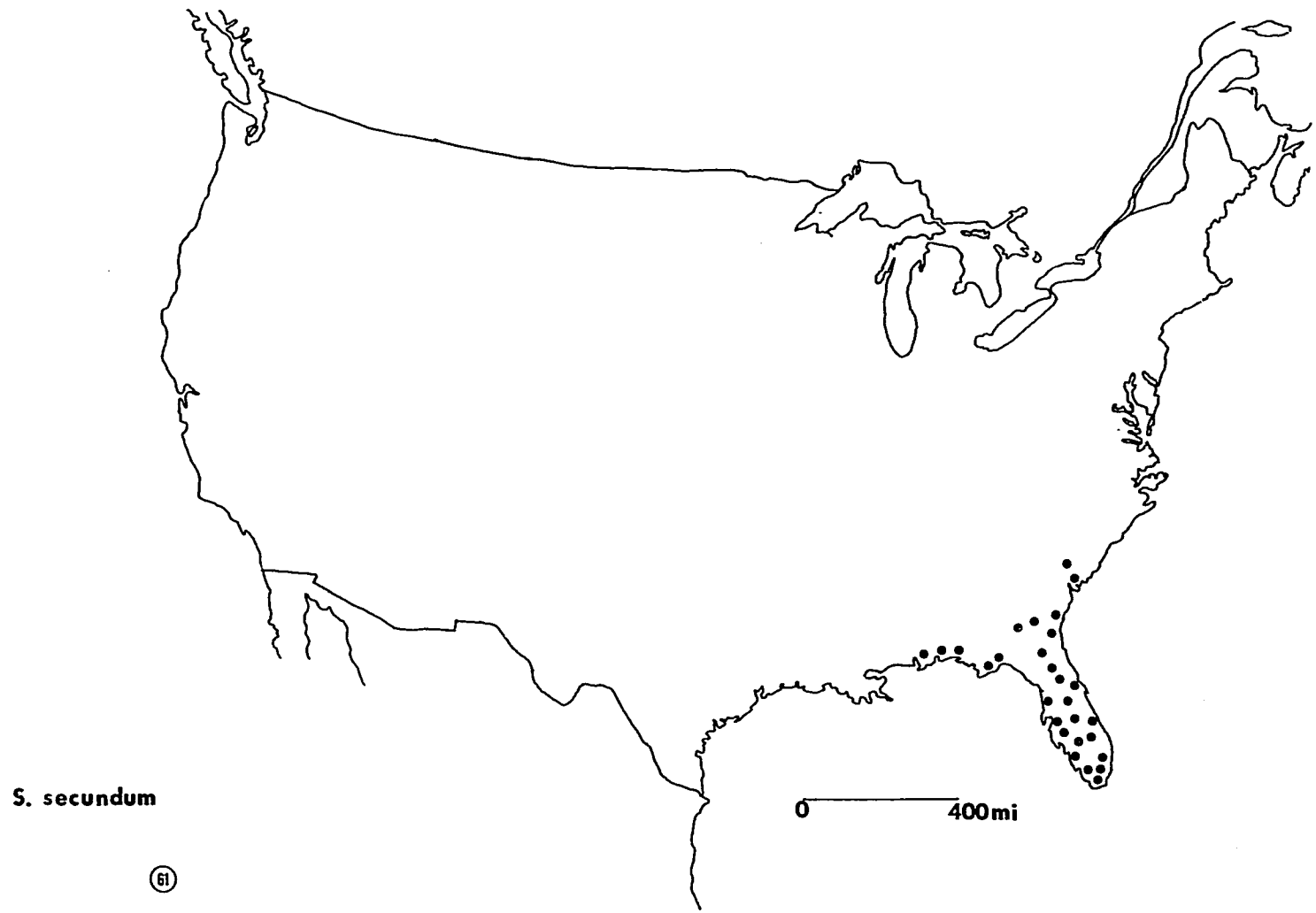
The nomenclatural history of Sorghastrum secundum seems fairly simple. New combinations were based on the different taxonomic conceptions of the genus Sorghastrum during different times.

Elliott in 1816, proposed the species Andropogon secundus. He

Figure 60. Sorghastrum secundum. A. Basal part, bar=5 cm. B. Inflorescence, bar=5 cm. C. Ventral view of the spikelet, bar=1 mm


B
C
A

Figure 61. Distribution of Sorghastrum secundum



S. secundum

(61)

suggested a close alliance to Andropogon nutans, basically differing by the presence of a 1-sided inflorescence in A. secundus. This author did not mention any type specimen.

Bentham (1881) proposed the genus Chrysopogon as having two natural sections. One of them, the section stipoides, included the American species in which the pedicellate spikelets were reduced to "long hairy stipes", rarely bearing a minute rudimentary glume. Based on this fact, Vasey (1883) suggested the new combination Chrysopogon secundus. Again, no type specimen was mentioned.

The new taxonomic conception of this genus, within the limits of Sorghum sensu lato is expressed in the combination, Sorghum secundum. This name was proposed by Chapman in 1883. No type specimen was mentioned.

Hackel (1889) proposed including this genus, within the boundaries of Andropogon suggesting the new name Andropogon unilateralis. This author denied the use of the epithet "secundum", considering Andropogon secundus Elliott, a later homonym of A. secundus Willdenow ex Nees (1829) and A. secundus (Presl) Kunth (1833). Andropogon secundus Willdenow ex Nees was described in 1829 and later published in Grisebach's Flora Brit. of West Indies in 1864. It is a synonym of Heteropogon contortus. On the other hand, Andropogon secundus (Presl) Kunth was published in 1830, and is a synonym of Trachypogon secundus Presl. Andropogon secundus Elliott is the earliest legitimate name. For the first time during the nomenclatural history of this species, some specimens were mentioned. Hackel cited specimens from Chapman, Garber, and Curtiss.

After Nash (1901) proposed the new genus Sorghastrum, the same author in 1903, suggested the new name combination Sorghastrum secundum which should be considered the legitimate name for this species.

I am considering the specimen from Florida collected by Curtiss 3644 (cited by Hackel in 1889), the Neotype of Sorghastrum secundum. The proposition of this Neotype specimen is based on the fact that in the original description of the present species, no type specimen was cited. The first specimen citation is Curtiss collection. Also, Garber and Chapman collections were mentioned, however no specification of locality or collection number was given.

14. Sorghastrum setosum (Grisebach) Hitchcock, Contrib. U.S. Natl. Herb. 12(6):195. 1909. Andropogon setosus Grisebach, Cat. Pl. Cub. 235. 1866. Type: BRAZIL. Brasiliae meridionalis, s.d., Sellow s.n. (Lectotype: US!). (Figs. 62A, 62B and 62C).

Sorghum parviflorum Desvaux, Hamilton Prodr. Pl. Ind. Occ. 12. 1825. Not Beauvois 1812. No type specimen cited.

Trachypogon stipoides (HBK) var. β Nees, Fl. Bras. 351. 1829. In part. Type: BRAZIL. Brasiliae meridionalis, s.d., Sellow s.n. (Lectotype: US!).

Andropogon francavillanus Fournier, Mex. Pl. 2:56. 1881. Type: BRAZIL. Brasilia, s.d., Riedel s.n. (Lectotype: US!).

Andropogon agrostoides Spegazzini, Anal. Soc. Cienc. Argent. 16:136. 1883. Type: ARGENTINA. Chaco, 20 Apr 1883, Spegazzini 12638

(Holotype: LP Photo!; US Fragm.!).

Sorghum nutans ssp. micranthum var. submuticus Hackel, Fl. Bras. 2(3):275. 1883. Based on Andropogon setosus Grisebach.

Andropogon nutans var. submuticus (Hackel) Hackel, DC. Monogr. Phan. 6:529. 1889. Based on Andropogon setosus Grisebach.

Andropogon nutans var. agrostoides (Spegazzini) Hackel, DC. Monogr. Phan 6:529. 1889. Based on Andropogon agrostoides Spegazzini.

Sorghastrum francavillanum (Fournier) Hitchcock, Contr. U.S. Natl. Herb. 12(6):195. 1909. Based on Andropogon francavillanus Fournier.

Sorghastrum agrostoides (Spegazzini) Hitchcock, Bot. Gaz. 51:300. 1911. Based on Andropogon agrostoides Spegazzini.

Sorghastrum parviflorum (Desvaux) Hitchcock & Chase, U.S. Natl. Herb. 18:287. 1917. Based on Sorghum parviflorum Desvaux.

Sorghastrum stipoides (HBK) Nash ssp. agrostoides (Spegazzini) Rosengurtt, Arrillaga & Izaguirre, Gramineas Uruguayas 201. 1970. Based on Andropogon stipoides HBK and Andropogon agrostoides Spegazzini.

Rhizome lacking. Culms slender, erect, (1.5-) 2.5-3.5 mm diam., 0.80-1.80 (-2.30) m tall. Internodes terete, smooth, glabrous, or slightly pubescent below the nodes. Leaves: blades convolute, 15-50 cm long, (2.5-) 4-8 mm wide, apex acute, margins serrulate, glabrous, or slightly pubescent on both surfaces; ligule 1.5-3.5 (-4.6) mm long, glabrous; sheaths 9-40 cm long, (1.8-) 2.5-4 (-5.2) mm wide, glabrous, or somewhat pubescent at the ligular area. Inflorescence a loose, erect

panicle, 10-40 cm long; rachis terete, glabrous; peduncle 15-50 (-81) cm long, glabrous. Spikelets dorsally compressed, 3.5-5 mm long; callus blunt, 2-2.5 mm long, silky villous. Glumes coriaceous; glume I truncate, usually (3.6-) 4-5 mm long and (0.6-) 0.9-1.3 mm wide, pubescent, 7-9-nerved; glume II acute, 3.5-5.5 mm long and (0.6-) 0.9-1.3 mm wide, glabrous, 5-nerved. Sterile lemma bifid, hyaline, 2.5-4 (-5) mm long, 0.5-1.5 mm wide, ciliate throughout the margins, 2-nerved. Fertile lemma hyaline, bifid, 2-4(-4.6) mm long, 0,5-1.0 mm wide, ciliate, 3-nerved. Awn straight or slightly twisted, usually non-geniculate, seldom once-geniculate, 1-12 mm long, usually 1.5 times longer than the spikelet. Anthers 1.5-3 mm long, yellow. Caryopsis 3-3.5 mm long. Sterile Pedicel 2-4.5 mm long, pubescent. Chromosome number 2n=20. Representative specimens examined: ARGENTINA. CORRIENTES: Ruta 12, 19 km de Corrientes, 22 Apr 1975, Schini & Mroginski 4654 (CTES); Ruta Nacional 12, 60 km E de Itati, Arrocera Rzepecki, 28 Feb 1977, Ahumada et al. 915 (F); 15 km E de Corrientes, Feb 18 1978, Ahumada et al. 1514 (CTES); Departamento Concepcion, Carambola, 21 Feb 1972, Pederson 10064 (NY); Ituzaingo, N of San Carlos, 11 Abr 1974, Krapovickas et al. 24962 (CTES); FORMOSA: Ruta 11, entre Dalmacia y Formosa, 24 Jan 1981, Petetin & Molina 1494 (BAB); MISIONES: Departamento Candelaria, Yalpichey, 21 Abr 1985, Montes 811 (NY); San Ignacio, 1 Mar 1946, Shurz 2131 (US); TUCUMAN: Departamento Capital, 12 Mar 1908, Lillo 38093 (NY). BELIZE. EL CAYO: Mountain Pine Ridge San Agustin, Jul-Aug 1936, Lundell 6865 (US). BOLIVIA. Ixiamas, 28 Dec 1901, Williams 1026 (NY, US); BUENA

VISTA: Departamento Santa Cruz, Prov. Sara, Mar 1921, Steinbach 5428 (US); Departamento Santa Cruz, Prov. Sara, 7 Apr 1925, Steinbach 7050b (US). BRAZIL. s.d., Riedel s.n. (NY, US); Brasilia, s.d., Sellow s.n. (INTA, LP); Brasilia meridionalis, s.d., Sellow s.n. (US): GOIAS: Rio de Prata, vicinity of Posse, 9 Apr 1966, Irwin et al. 14553 (NY); MATO GROSSO: Mun. de Barra de Garcas, 250 km along new road NNE of village of Xavantina, 3 Sep 1968, Eiten & Eiten 8549 (MO); 8 km of the base camp of the expedition, 270 km N of Xavantina on the Xavantina-Sao Felix road, 21 Jun 1968, Ratter et al. 1893 (NY); MINAS GERAES: near Rio de Peixa, Serra do Cipo, 28 Mar 1925, Chase 9188 (NY); PARANA: Mun. Jagtuariaiva, Barra do Rio das Montes, Rio Jaguariaiva, 18 Jan 1965, Smith & Klein 14746 (US); RIO GRANDE DO SUL: Las Pelotas, 3 Oct 1954, Costa Sacco 92 (US); Brasilia, Sao Leopoldo, Feb 1918, Malne 1394 (US); SANTA CATARINA: Curitibanos, 22 Feb 1962, Reitz & Klein 12233 (US); Cruzeiro, 17 Jan 1957, Smith & Reitz 10263 (US). COSTA RICA. GUANACASTE: Hda. Murcielago, road near CIA, S of la Cruz, 26 Jul 1971, Pohl 12650 (F). COLOMBIA. META: Loma linda, al SE de San Martin, 15 Sep 1966, Robinson 3084 (US). CUBA. near St. Spirictus, 27 Aug 1909, Leon 895 (US); N of St. Spirictus, 9 Aug 1915, Leon 5365 (US). GUATEMALA. PETEN: Dolores, about 2 km E of village, 11 Sep 1961, Contreras 2880 (TEX, US); La Libertad, finca Buenos Aires, 26 Jul 1980, Crowe 444 (F). GUIANA. Rufuneni Savanna, s.d., Melville 103 (US). HAITI. Las Cahobas, 29 Aug 1917, Cook et al. 98 (US). HONDURAS. vicinity of Siguatepeque, 5 Aug 1936, Yuncker 6351 (NY); MORAZAN: Region of Las Mesas, 2 Oct 1949, Standley 24027 (F). JAMAICA. Halls' Delight, St. Andrew, 22 Jul 1916,

Harris 12394 (NY). MEXICO. Consoquitla, Aug 1841, Liebmann 401 (F); Mirador, Aug 1841, Liebmann 36 (MO); CHIAPAS: Aguacate, Palenque, 16 Jul 1939, Matuda 3770 (US); 70 km al N de San Cristobal de las Casas, Mun. de Oxchuc, 26 Oct 1985, Davila et al. 204 (ISC); 10 km al N de Ocosingo, Mun. de Ocosingo, 26 Oct 1985, Davila et al. 205 (ISC); VERACRUZ: Orizaba, s.d., Botteri s.n. (US); 3 km antes de Lencero, Carr. Jalapa-Veracruz, 15 Oct 1972, Dorantes et al. 1677 (F): between Coatepec and Jalapa, 4 Sep 1910, Hitchcock 278 (NY, US); Mun. de Dos Rios, Miradores, 11 Sep 1974, Ventura 10524 (ENCB); SAN LUIS POTOSI: El Charco, Mun. de Ciudad del Maiz, 15 Jan 1982, Bravo 163 (COT); TABASCO: s.d., Rovirosa 1002 (US); 3 km S of the Colegio Superior de Agricultura Tropical, 21 km W of Cardenas, 15 Aug 1974, Conrad & Conrad 2960 (ISC). NICARAGUA. La Tronquera cerca de Rio Leicua, 19 Aug 1965, Molina 14939 (F); CHONTALES: 5 km SW of Santo Tomas, 18 Jul 1970, Pohl 12338 (F). PARAGUAY. Central Paraguay, s.d., Morong 545 (MO); near Villa Rica, s.d., Jorgensen 4097 (SI); Gran Chaco, Santa Elena, Jan 1903, Hassler 2731 (NY); Puerto Casado, Chaco Paraguayo, Feb 1931, Rojas 5592 (US); CONCEPCION: orilla del Rio Paraguay, Puerto Fonciere, 20 Jan 1942, Rosengurtt B-5490 (US). PUERTO RICO. Vicinity of Vega Baja, 7 Nov 1913, Chase 6421 (US); Happy Hollow, road to Trujillo Alto, vicinity of San Juan, 9 Dec 1913, Chase 6773 (US). SANTO DOMINGO. MONTE CRISTI: Monviou, Cordillera Central, 30 May 1929, Ekman 12687 (US). VENEZUELA. BOLIVAR: Cuchivero del Tigre, cerca del Rio Cuchivero, 17 Jun 1940, Williams 13348 (F); T.F.A.: Distrito Atures, San Juan de Manapiare, E del Rio Manapiare, 13 Oct 1977,

Huber 1099 (NY); Distrito Atures, 8 km S of Puerto Ayacucho, 13 Apr 1978, Davidse & Huber 14949 (MO).

Sorghastrum setosum has a very small awn, less than 12 mm long. Often, individuals have a mucronate lemma instead of a real awn. The awn, if present, is usually non-geniculate; however, some individuals may have a once-geniculate awn. The mature panicle very lax, but in some individuals (probably immature inflorescences) it is more or less dense.

This species is very well distributed in the tropical and subtropical zones of the Americas (Fig. 63). It is present from the northeast of Mexico, across the Sierra Madre Oriental to Chiapas. S. setosum is also represented in Central America and the Caribbean Islands. In South America it occurs from Colombia and Venezuela to Brazil, Uruguay, Paraguay, Bolivia and Argentina. S. setosum does not extend to the western part of South America, probably because of the natural Andean barrier. This species has a wide altitudinal range, from sea level up to 1500 m. However, S. setosum occurs mainly at the lower part of the mountains.

Sorghastrum setosum, along with S. trichopus in Africa, is well adapted to marshy and flooded areas. That is the case in most of the Cerrados of Brazil, the coast of the Gulf of Mexico, the savannas of South America, as well as sandy and wet places of Central America and West Indies.

Sorghastrum setosum flowers principally from July to October in the Northern Hemisphere, and from January to March in the Southern Hemisphere. The flowering period, in both cases, corresponds to the

Figure 62. Sorghastrum setosum. A. Basal part, bar=5 cm. B. Inflorescence, bar=5 cm. C. Ventral view of the spikelet, bar=1 mm


A
B
C

Figure 63. Distribution of Sorghastrum setosum


S. setosum
0
500 mi
63

autumn season.

Sorghastrum setosum is closely related to S. trichopus. Morphologically, both species are very similar. S. setosum and S. trichopus have the shortest awn of all the species. The leaf anatomy of these species has many features in common, especially in relation with the midrib (See anatomy). Also, both species seem to have similar environmental requirements. They are well adapted to marshy and flooded areas. I speculate that the ancestral population of these two species was split during the separation of Gondwanaland. Having a common gene pool both were able to spread along wet and marshy zones.

NOMENCLATURE:

In 1825 Desvaux suggested the name Sorghum parviflorum for this species; however, this name turned out to be a later homonym of Sorghum parviflorum Beauvois (1812), which was based on a different taxon. For this reason this homonym must be rejected as illegitimate (Art. 72, ICBN).

Trachypogon stipoides (HBK) Nees was proposed in 1829. It is really a group of different varieties that are now considered to be different species. Only variety "β" of T. stipoides corresponds to the present S. setosum. However, the epithet "stipoides" cannot be used for this species, because it is based on Andropogon stipoides HBK (1816). The description of A. stipoides does not fit the present species, but with the real Sorghastrum stipoides.

Grisebach (1866) transferred variety "β" of Trachypogon stipoides to Andropogon setosus. As did many other botanists of last century,

Grisebach included Sorghastrum within the wide and uncertain limits of Andropogon sensu lato.

Based on the fact that neither the Desvaux, nor Nees species names can be used, the basionym and consequently the type of this species should be Andropogon setosus Grisebach.

Within the genus Andropogon, Fournier (1881), separated five sections. Within section Sorghastrum, the new species Andropogon francavillanus Fournier was described. Specimens from Mexico (Veracruz) and Brazil that were cited fit into the boundaries of Andropogon setosus.

The same kind of situation is recorded for Andropogon agrostoides, described by Spegazzini (1883). Andropogon agrostoides is based on a specimen from the Chaco region that corresponds again to Andropogon setosus.

In 1883, Hackel included many Sorghastrum species within Sorghum nutans, separating them into subspecies and varieties. This species was included in Sorghum nutans ssp. micranthum var. submuticus Hack. However, the same author in 1889, transferred it back to Andropogon nutans var. submuticus (Hack.) Hack. and to Andropogon nutans var. agrostoides (Speg.) Hack. The difference pointed out between these two varieties is the length of the spikelet. The former has shorter awns than the latter one.

Hitchcock (1909), based on Fournier's A. francavillanus and already accepting the genus Sorghastrum as valid, suggested the new combination Sorghastrum francavillanum (Fourn.) Hitchc. In the same publication,

Catalogue of the Grasses of Cuba, the author also proposed the new combination Sorghastrum setosum (Griseb.) Hitchc., which represents the valid name for this species.

In 1911 and 1917, Hitchcock suggested two other new combinations respectively. Sorghastrum agrostoides (Desv.) Hitchc., based on A. agrostoides Speg., and Sorghastrum parviflorum (Desv.) Hitchc. based on Sorghum parviflorum (Desv.) Hitchc.

Finally, Rosengurtt et al. (1970) transferred this species to Sorghastrum stipoides (HBK) Nash ssp. agrostoides (Speg.) Rosengurtt. Rosengurtt's species is based in Andropogon stipoides HBK and Andropogon agrostoides Speg, which are synonyms of two well recognized species: Sorghastrum setosum and Sorghastrum stipoides, respectively. See discussion of S. setosum and S. stipoides.

15. Sorghastrum stipoides (HBK) Nash, N. Amer. Fl. 17:129. 1912. Andropogon stipoides HBK, Nov. Gen. Sp. 1:189. 1816. Type: COLOMBIA. Nova Granada, between Popayan and Almaguer, Socobini, s.d., HBK 9 (Holotype: US Frag.!). (Figs. 64A, 64B and 64C).

Trachypogon stipoides (HBK) Nees var.γ, Fl. Bras. 351. 1829. In part. Based on Andropogon stipoides HBK.

Andropogon humboldtianus Steudel, Syn. Plan. Glum. 1:392. 1855. Based on Andropogon stipoides HBK.

Andropogon rufidulus Steudel, Syn. Plan. Glum. 1:392. 1855. Based on Trachypogon stipoides Nees.

Sorghum nutans ssp. avenaceum var.β stipoides Hackel, Fl. Bras. 2(3):274. 1883. Based on Andropogon stipoides HBK.

Andropogon nutans ssp. avenaceum var. γ burchellii Hackel, Fl. Bras. 2(3):274. 1883. Type: BRAZIL. between Funil et St. Joao, s.d., Burchell 8927 (Holotype: US!).

Sorghum nutans ssp. micranthum var. α genuinum Hackel, Fl. Bras. 2(3):274. 1883. Based erroneously on Trachypogon stipoides var. Nees.

Andropogon nutans var. stipoides (Kunth) Hackel, DC. Monogr. Phan. 6:530. 1889. Based on Andropogon stipoides HBK.

Sorghastrum stipoides ssp. stipoides Rosengurtt, Arrillaga & Izaguirre, Gramineas Uruguayas 201. 1970. Based on Andropogon stipoides HBK.

Rhizomes lacking. Culms erect, simple, caespitose, (1-) 2-4 (-5) mm diam., 0.70-1.50 m tall. Internodes terete, smooth, glabrous, sometimes slightly pubescent below the nodes. Leaves: blades flat, linear, acuminate, (10-) 20-60 cm long, (1-) 3-9 mm wide, glabrous or pubescent on either surfaces, margins serrulate; ligule subcoriaceous, 1.5-3.5 (-4.5) mm long; sheaths striate, 15-30 (-47) cm long, 1-6 mm wide, glabrous, sometimes slightly pubescent at the ligular area. Inflorescence an open, loose panicle, erect or sometimes nodding, 15-40 (-50) cm long; rachis terete, pubescent; peduncle glabrous, (14-) 30-50 (-60) cm long. Spikelets dorsally compressed, narrowly lanceolate, 4-5.5 mm long; callus blunt, villous, about 2 mm long. Glumes equal, coriaceous; glume I oblong-lanceolate, truncate, 3-5 mm long, 1-1.5 mm wide, pubescent, 7-9-nerved; glume II lanceolate, acute, 3.5-5.5 mm long,

1-1.5 mm wide, glabrous, 5-nerved; Sterile lemma linear-oblong, hyaline, bifid, 3-4.5 (-5) mm long, 0.5-1.3 mm wide, ciliate, 2-nerved; Fertile lemma oblong, bifid, hyaline, 25-45 mm long, 0.6-1.2 mm wide, ciliate, 3-nerved. Awn frequently once-geniculate, rarely twice-geniculate, 1-2.5 cm long, about 3 times longer than the spikelets. Anthers 2-3.5 mm long. Sterile Pedicel 2-4 cm long. Caryopsis 1-1.5 mm long. Chromosome number 2n=20.

Representative specimens examined: ARGENTINA. CHACO: Campo del Cielo, Capdevila, 8 Dec 1946, Schulz 925 (MO); FORMOSA: Pilcomayo, ruta 86 al S, a 2 km del Km 50, 1 Apr 1948, Morel 5237 (US); JUJUY: San Salvador de Jujuy, 19 Feb 1953, Hunziker & Caso 6131 (BAB); MISIONES: Apostoles, San Jose, 20 Feb 1946, Bertoni 2728 (US); SALTA: Quebrada del Rio Grande, Guachipas, 1 May 1942, Hunziker 1794 (BAB). COLOMBIA. Santa Marta, 1898-1899, Smith 2122 (LL, MO, NY, TEX, US); BOLIVAR: Cerro San Lucas, between Aguas Zembradas and Pinal, 8 Dec 1944, Drew E-748 (US); CAUCA: El tambo, Hoya del Patia, Corregimiento de Mosquera, Hacienda Aguaclara y sus alrededores, Aug 1949, Idrobo & Fernandez 85 (US); META: Puerto Lopez, Hacienda San Cayetano, al lado de la carretera a Villaviscencio, 24 Sep 1963, Blydenstein 1711 (F, MO, NY). BOLIVIA. Gebusch der Derge um Vallegrande, Mar 1911, Herzog 1789 (US); Larecaja, Sorata, Mar-Apr 1858, Mandon 1382 (NY); SANTA CRUZ: Ichilo, Buena Vista to Rio Surutu, 19 Mar 1981, Renvoize & Cope 3984 (US). BRAZIL. DISTRITO FEDERAL: Brasilia, D.F. Estacao Experimental deo Instituto Central de Biologia, Apr 1968, Lima & Herringer 193 (NY, US); 3 km W of the Goias-Distrito Federal border along Hwy Br-020-030, 9 Apr 1976, Davidse et al. 12169

(CHAPA, MO); GOIAS: Goyandra, 26-27 Mar 1930, Chase 11579 (US); MATO GROSSO: between Campo Grande and Dourados, 14-17 Feb 1930, Chase 10898 (US); Corego de Porco, 240 km N of Xavantina on Xavantina-Sao Felix road, 7 May 1968, Ratter et al. 1340 (US); MINAS GERAES: Corinto, Fazenda do Diamante, 4 Apr a1931, Mexia 5542 (MO, NY, TEX): Sao Joaquim, Curral Falso, Bom Jardin, 10 Dec 1958, Reitz & Klein 7732 (US); PARANA: Contenda, 4 Nov 1966, Hatschback 15242 (F, MO); Ponta Grossa, Jan 28 1946, Swallen 8305 (US);Sierra do Oratorio, 23 Oct 1958, Reitz & Klein 7454 (US). RIO GRANDE DO SUL: Vacaria, 14 km de Vacaria, rumbo Bom Jesus, 25 Sep 1961, Pabst 6331 (US). ECUADOR. CARCHI: Alor Hcda. San Rafael, faldas occidentales de la Cordillera, 5 Apr 1952, Solis 21017 (US); PICHINCHA: Quito, below Guapulo, 31 May 1939, Asplund 6638 (US); alrededores Quito, Reg. Interandina, 15 Dec 1945, Solis 11329 (F, US). PERU. Cuzco, 11 May 1930, Bues s.n. (F); CELENDIN: Dtto. Cajamarca, Canyon of the Rio Maranon above Balsas, 5 km below summit of the road to Celendin, 16 May 1964, Hutchinson & Wright 5384 (F, NY). SURINAME. Sipaliwini savanna, 25 Aug 1966, Donselaar 3580 (US). URUGUAY. Tacuarembo, Tres Cruces, Feb 2 1962, Millot 1267 (US). VENEZUELA. 1842-1843, Funcke 431 (W).

Sorghastrum stipoides is distinguished by the semi-open panicle, with pale (yellowish) spikelets. Usually the individuals of this species have pubescent leaves and rachis. S. stipoides can be confused with S. scaberrimum, however, the latter has very dark spikelets and sometimes scabrous leaves, but rarely has any pubescence. Also S. stipoides

inhabits places mostly below 1000 m and always associated with the Andean Mountains. On the other hand, S. scaberriumum is located mainly above 1000 m, up to 2500 m in the Brazilian Highlands.

In addition to the similarities between these two species, S. stipoides may also be confused with S. setosum. However, the former has longer awns than the latter species. S. setosum is located from Mexico to Brazil (eastern regions of South America), meanwhile S. stipoides inhabits the low parts of the Andean regions (N, NW zones of South America).

Sorghastrum stipoides occurs in Colombia, Venezuela, Peru, Bolivia, as well as northern Argentina and Brazil (Fig. 65). It inhabits low parts of the Andean regions. Probably this natural barrier has inhibited the further migration to western and northern regions.

Sorghastrum stipoides inhabits low areas. It is always associated with the Andes. This species may grow in dry savannas, in red argillaceous soils. Sometimes the present species may also occur in wetter places, such as swamp edges, pine forest edges or even moist valleys.

Sorghastrum stipoides flowers from February to May in the Southern Hemisphere and usually from August to November in the Northern Hemisphere. In both cases the flowering period takes place in the autumn season. The altitudinal range is usually below 1000 m, often individuals of this species may occur at sea level.

Sorghastrum stipoides is related to S. scaberrimum. They are morphologically and anatomically similar. However, the latter is

Figure 64. Sorghastrum stipoides. A. Basal part, bar=5 cm. B. Inflorescence, bar=5 cm. C. Ventral view of the spikelet, bar=1 mm

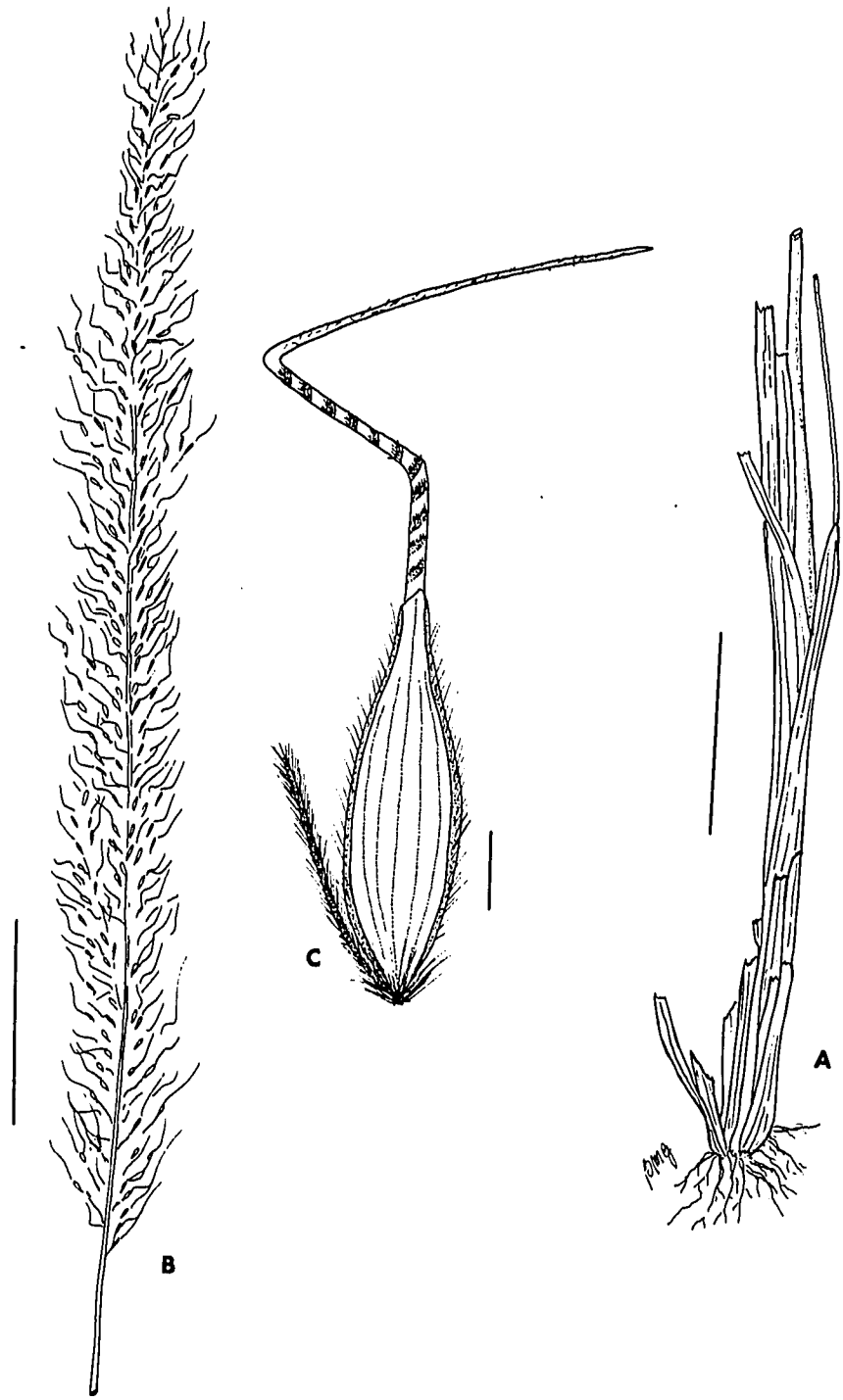

B
C
A

Figure 65. Distribution of Sorghastrum stipoides


S. stipoides
65
0
600 mi

inhabiting higher elevations than S. stipoides. The phylogenetic analysis shows that S. stipoides might probably represents the connection with the North American species.

NOMENCLATURE:

In 1816, Humboldt, Bonpland and Kunth proposed the new species Andropogon stipoides. It is based on a specimen from Colombia. The authors pointed out as distinguishing characters of the species, the pubescence of rachis and pedicel. This name is the basionym of the present species, and subsequently the Colombian specimen is the Holotype.

Nees (1829) included various Sorghastrum species within Trachypogon stipoides. His variety "γ", characterized by a pubescent rachis, fits with the present species.

Andropogon humboldtianus was a new name suggested by Steudel 1855. The author cited A. stipoides HBK as a synonym of his species. I think that he tried to narrow the limits of the present species. However, the description fits A. stipoides HBK. In the same publication, Synopsis Plantarum Glumacearum, Steudel proposed the new species Andropogon rufidulus, citing as a synonym the species Trachypogon stipoides Nees. In both cases, Steudel proposed superfluous names (Art. 63, ICBN) for Andropogon stipoides.

Many Sorghastrum species were included as subspecies and varieties of Sorghum nutans (Hackel, 1883). The present species was called Sorghum nutans ssp. avenaceum var. β stipoides and var. γ Burchellii. The difference between these two varieties is based on the pubescence of the rachis. In the former the rachis is pubescent, whereas in the latter it

is glabrous. However, examining the type of variety Burchellii it was found that the rachis is also pubescent. In the same publication, Flora Brasiliensis, Hackel suggested Sorghum nutans ssp. micranthum var. genuinum which also corresponds to the present species.

Hackel (1889) included in the limits of Andropogon nutans L, those species formerly considered by himself (1883), within Sorghum nutans. The author called the present species Andropogon nutans var. stipoides which is based on Andropogon stipoides HBK.

After the Nash (1901) transfer to the genus Sorghastrum, the same author proposed the new combination Sorghastrum stipoides. This is the legitimate name that is based on the basionym Andropogon stipoides HBK.

Finally, Rosengurtt et al. (1970) suggested the name Sorghastrum stipoides ssp. stipoides for this species. They also proposed Sorghastrum stipoides ssp. agrostoides. However, in this work these two subspecies are considered two different species: Sorghastrum setosum and Sorghastrum stipoides.

16. Sorghastrum trichopus (Stapf) Pilger, Eng. & Prantl. Pflanzen. ed. 2, 14e:142. 1940. Andropogon trichopus Stapf, Kew Bull. 287. 1897. Type: NIGERIA. Niger region, Nupe, in open plains, s.d., Barter 1375 (K). Not seen. (Figs. 66A, 66B and 66C).

Andropogon nutans L. var africanus Franchet, Bull. Soc. Hist. Nat. Autun. 8:329. 1895. Type: FRENCH CONGO. Les prairies fertiles a Bouanga, s.d., Thollon 1077 (Lectotype: K?); Ogoove, plaine de Lope, s.d., Thollon 788 (Syntype: P?). Not seen.

Andropogon nutans L. var angolense Rendel, Cat. Afr. Pl. Welw. 2(1):152. 1899. Type: ANGOLA. HUILLA: rather damp wooded meadows between Lopollo and Catumba, Feb 1860, Rendle 7491 (lectotype: BM?). Not seen.

Andropogon friessii Pilger, Ergeb. Schwed. Rhod. Kongo Exped. 1:195. 1915. Type: RHODESIA. Bangeolo bei Kamindas, 9 Oct, Rosen 965 (Holotype: B?). Not seen, probably destroyed.

Sorghum trichopus (Stapf) Stapf, Flora of Tropical Africa 9:141. 1919. Based on Andropogon trichopus Stapf.

Sorghum micrantherum Stapf, Fl. Trop. Afr. 9:142. 1919. Based on Andropogon nutans L. var angolense Rendle.

Sorghum pogonostachyum Stapf, Fl. Trop. Afr. 9:144. 1919. Type: ANGOLA. BENGUELLA: Country of the Ganguellas and Ambuellas, s.d., Gossweiler 2225 (Holotype: K!).

Sorghum friesii (Pilger) Hubbard, Kew Bull. Misc. Inf. 109. 1934. Based on Andropogon friesii Pilger.

Sorghastrum friesii (Pilger) Pilger, Notiz. Bot. Gart. Berlin 14:96. 1938. Based on Andropogon friessii Pilger.

Sorghastrum micrantherum (Stapf) Pilger, Engl. & Prantl. Pflanzenfam, ed. 2. 14e:142. 1940. Based on Andropogon micrantherum Stapf.

Miscanthidium gracilius Napper, Kirka 3:120. 1963. Type: TANZANIA. Msima, s.d., Emson 371 (Holotype: K?). Not seen.

Sorghastrum pogonostachyum (Stapf) Clayton, Kew Bull 30(3):509. 1975. Based on Sorghum pogonostachyum Stapf

Rhizome creeping, tufted and with intravaginal innovation-shoots. Culms erect, slender and smooth, 2-3 mm diam., 1.50-1.70 m tall. Internodes terete, smooth, glabrous or slightly pubescent below the nodes. Leaves: blades flat or convolute, 15-30 cm long, 3-5.5 mm wide, glabrous, scarious or slightly hairy, wider at the base, where they are abruptly contracted, margins serrulate; ligule 1.5-3.5 mm long, pubescent; sheaths firm, tight, 15-25 cm long, 2.5-4 mm wide, glabrous, almost always including the nodes. Inflorescence usually an open panicle, lower branches very distant, 10-25 cm long; rachis and branches smooth and glabrous; peduncle 25-40 cm long, glabrous. Spikelets dorsally compressed, narrowly lanceolate, 5-7 (-9) mm long; callus pointed, long-bearded, up to 4 mm long. Glumes equal, coriaceous; glume I 5-6.5 mm long, 1.2-1.6 mm wide, pubescent, 7-9-nerved; glume II 5-7.5 (-9) mm long, 1-1.5 mm wide, glabrous, 5-nerved. Sterile lemma linear-oblong, hyaline, 4.5-6 mm long, 0.8-1.2 mm wide, ciliate, 2-nerved. Fertile lemma oblong, bifid, hyaline, 4-5.5 mm long, 0.8-1 mm wide, ciliate, 3-nerved. Awn straight or slightly geniculate, 6-10 mm long, usually 1.3 times longer than the spikelet. Anthers 1.5-3.5 mm long. Caryopsis 2.5-3.5 mm long. Sterile Pedicel 4-5 mm long, pubescent. Chromosome number 2n=40.

Specimens examined: BECHUANALAND. BOTSWANA: Depenga Island, 20 Apr 1976, Smith 1698 (MO); 11 km S of Gomare on road to Nokaneng, 18 Mar 1976, Ellis 2680 (MO); Thaoge river, 11 Apr 1976, Smith 1685 (MO). NIGERIA. 14 miles S of Damaturu, 27 Aug 1964, Deleeuw 1133 (US).

RHODESIA. Rusape road, 22 Jan 1949, Fisher & Schweickerdt 490 (B, MO); MATOPO: Mt. Sheleli road, 4 km N of Mt. Sheleli Dam, 16 Jan 1973, Simon 2310 (MO); NORTHERN: Lediba at Matsandi Aga Mtalelo Island, 30 Mar 1973, Smith 503 (MO); SALISBURY: Greystone Park, 4 Feb 1974, Bezuidenhaut 41 (MO); WANKIE: Victoria Falls National Park, 29 Jan 1974, Gonde 32/74 (MO). SOUTH AFRICA. TRANSVAAL: Mosdene Farm, Naboomspruit, 22 Feb 1974, Germinshuizen 61 (MO); NYLSTROOM: Farm Mosdene, flooded areas, 12 Feb 1980, Smook & Russell 1957 (MO). ZAMBIA. Kasama Dambo, 55 kms E-SE of Mporokaso, 13 May 1962, Robinson 5180 (B); Nawala, Cordon Rd., near Musa River, 28 Jan 1962, Mitchell 12/78 (B); VICTORIA: Makoli Exp. Farm, 27 Jan 1948, Robinson 18906 (NY); Livingston Island, 26 Mar 1976, Ellis 2794 (MO). ZIMBAWE. 30 Mar 1973, Chiparawasha 665 (MO).

Sorghastrum trichopus has very short awns. Usually the awn is straight, rarely once-geniculate. This species can be confused with Sorghatrum setosum which also has short and weak awns. However, S. trichopus has a smaller awn/spikelet proportion, a sharper callus, as well as a completely different distribution pattern. Also, the anatomical studies carried out show the existence of two different anatomical patterns.

This species is distributed in the African continent (Fig. 67). It is mainly located at the south and southeast of Africa in the countries of Angola, Bechuanaland, Rhodesia, Zambia, and South Africa. This species has an altitudinal range from 1000-1500 m. It grows on the mountain chains of Muchinga, Katanga, Cebombo, and others.

Sorghastrum trichopus is well adapted to marshy and flooded areas.

It grows in wet edges of woodlands and grasslands, sometimes it may be located in sandy places. It flowers from December to April, which corresponds to the autumn season in the Southern Hemisphere.

Sorghastrum trichopus presents similar morphological features and habitat characteristics as S. setosum. These species are closely related. I think that the ancestral population of these two species was split during the separation of Gondwanaland. Both populations with similar gene pools successfully established in wet and marshy places.

NOMENCLATURE:

When the genus Sorghastrum was included within the boundaries of Andropogon sensu lato, Franchet (1895) adopted the idea of Hackel (1889) of including most Sorghastrum species as varieties of Andropogon nutans. This author suggested the name Andropogon nutans var. africanus for the present species. It is based on a specimen from French Congo collected by Thollon 1077. The name A. nutans is a misapplication of the Linnean North American species.

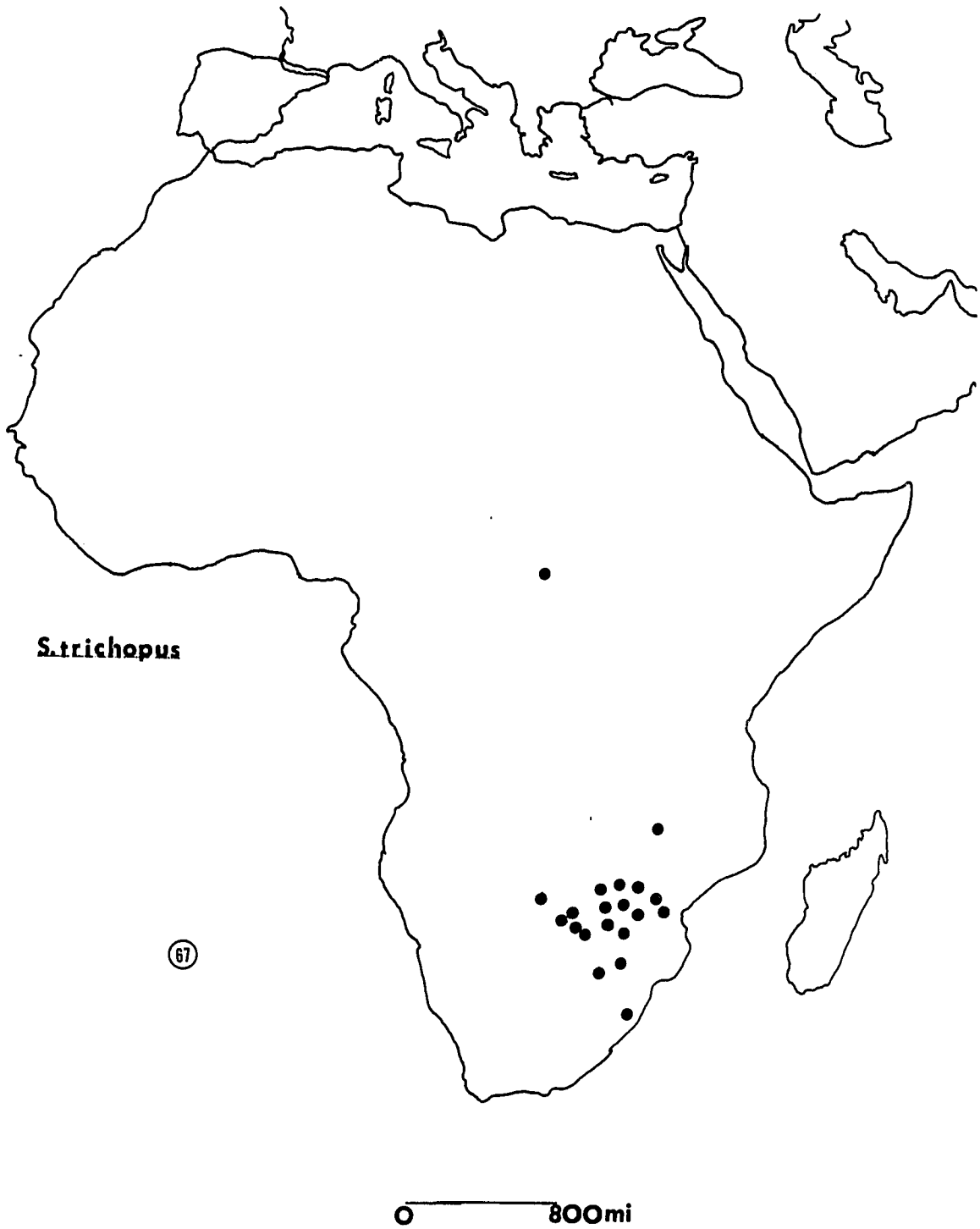
Stapf (1897) proposed the name Andropogon trichopus for this species. It is based on a specimen from Nigeria (Barter 1375). This name should be considered the basionym of the present species. Consequently Barter's specimen represents the type specimen.

Pilger (1915), suggested the name Andropogon friesii for the present species. It is based on a specimen from Rhodesia (Rosen 965). This specimen was not found, but I suppose it was deposited in (B) and probably was destroyed.

Figure 66. Sorghastrum trichopus. A. Basal part, bar=5 cm. B. Inflorescence, bar=5 cm. C. Ventral view of the spikelet, bar=1 mm


A
C
B

Figure 67. Distribution of Sorghastrum trichopus


S.trichopus
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800mi

Sorghum nutans var. angolense, was another name for this species proposed by Rendle (1899). He followed Hackel (1883) who included Sorghastrum species as subspecies of Sorghum nutans. Rendle mentioned that the variety "angolense" as close to Hackel's American variety "avenaceum", but was distinguishable by the shorter awn and more open panicle.

Stapf (1919) did not accept the rank of variety proposed by Rendle (1899) and suggested the new name Sorghum micrantherum for the present species. In the Flora of Tropical Africa, he suggested a new species, Sorghum pogonostachyum based on a specimen from Angola, (Gossweiler 2225). However, both the description and the specimen agree with his species Sorghum micrantherum. The same author, in the same publication, proposed the new combination Sorghum trichopus which is based on A. trichopus (basionym of the legitimate species).

Hubbard (1934) included the present species within Sorghum. Based on Andropogon friesii Pilger, the author suggested the new combination Sorghum friesii.

After the genus Sorghastrum was proposed by Nash (1901), many new combinations were suggested. Pilger (1938) proposed the name Sorghastrum friesii, based on Andropogon friesii.

Sorghastrum micrantherum was the new combination suggested by Pilger, which is based on Andropogon micrantherum proposed by Stapf in 1919. In the same publication, Pilger also proposed the new combination Sorghastrum trichopus based on Andropogon trichopus. This is the legitimate name of the present species at this rank. The type specimen

is the specimen collected by Barter, in Nigeria.

In 1963, Napper published the species Miscanthidium gracilius. He mentioned the existence of a mixture of pedicelled spikelets and barren pedicels in its inflorescence. However, the description fits within the limits of the present species. I think that he confused the genera Miscanthidium (with a tough rachis and both spikelets pedicelled) and Sorghastrum (with a fragile rachis, one sessile spikelet and usually a barren pedicel).

Finally, Clayton (1975) proposed the new combination Sorghastrum pogonostachyum which is based on Sorghum pogonostachyum Stapf that is considered a synonym of the present species.

17. Sorghastrum viride Swallen, Phytologia 14(2):98. 1966. Type: BRAZIL. SAO PAULO: das Sete Lagoas, Mun. de Moji-Guacu, 20 Sep 1960, Eiten & Eiten 2336 (Holotype: US!; Isotypes: F!; NY!). (Figs. 68A, 68B and 68C).

Rhizome lacking. Culms erect, caespitose, stout, 2-5 mm diam., 0.80-1.70 (-2.0) m tall. Internodes terete, smooth, glabrous. Leaves blades: flat, linear, 15-50 (-70) cm long, 2-9 mm wide, acute, frequently glabrous, seldom slightly pubescent, margins serrulate; ligule membranous, 3-4 mm expanding into very obvious auricles up to 7 mm long; sheaths 15-35 cm long, 2-6 mm wide, frequently glabrous, sometimes pubescent. Inflorescence an erect panicle, at maturity somewhat nodding, 15-40 cm long; rachis terete, glabrous; peduncle 20-50 (-60) cm long, glabrous. Spikelets dorsally compressed, lanceolate, yellow or yellow-

greenish, (4.5-) 5-6.8 mm long; callus blunt, villous. Glumes coriaceous, shining; glume I truncate, 4.5-6.5 mm long, 1.2-1.6 mm wide, pubescent, 7-9-nerved; glume II acute, 4.5-6.8 mm long, 1-1.7 mm wide, glabrous, 5-nerved. Sterile lemma hyaline, bifid, 3-5 (-6) mm long, 0.5-1.7 mm wide, 2-nerved. Fertile lemma hyaline, bifid, 3-5 mm long, 0.5-1 mm wide, 3-nerved. Awn twice geniculate, 1.5-2.5 (-3) mm long, about 3-4 times longer than the spikelet. Anthers 2-3.5 mm long. Caryopsis 2-3 mm long. Sterile Pedicel 2-4.5 mm long, pubescent. Chromosome number 2n=20.

Specimens examined: ARGENTINA. CHACO: Dtto. San Fernando, Fontana, s.d., Meyer 69 (CTES); CORRIENTES: Dtto. Ituzaingo, Isla Apipe Grande, Panco Cue, 5 Oct 1978m Schinini & Vanni 15804 (CTES); Dtto. Ituzaingo, Ruta 12, 5 km de Ayo, Itaembe, 23-24 Oct 1974, Tressens et al. 415 (CTES); Dtto. Ituzaingo, 15 km E de Ruta Nac. No. 12 camino a San Carlos, 11-12 Feb 1971, Krapovickas et al. 18072 (BAB, LL, SI); Dtto. Sto. Tome, cca. de Sto. Tome, Oct 1977, Cabrera 28407 (SI); Dtto. Sto. Tome, Estancia Garruchos, potrero Curuzu, 7 Feb 1972, Quarin 465 (CTES); Dtto. Santo Tome, Rio Aguapey y Ruta 14, 7 Dec 1974, Quarin et al. 2658 (US); Dtto. Sto. Tome, Ruta 37, 5 km E de Gdor. Virasoro, 12 Nov 1974, Schinini & Carnevali 10557 (CTES); Dtto. Sto. Tome, 15 km de Virasoro, camino a Garruchos, 5 Feb 1972, Quarin 417 (CTES, SI); ENTRE RIOS: Federacion, Salto Grande, 12 Dec 1965, Burkart & Troncoso 26202 (SI); MISIONES: 17 km de San Javier a Alm, 14 Nov 1976, Correa et al. 7010 (BAB); Dtto. Candelaria, Santa Ana, 28 Sep 1945, Montes 1145 (US, WIS); Dtto. San Ignacio, Colonia Corpus, 20 Oct 1948, Schwarz 6450 (US, WIS); Dtto. San

Ignacio, Santo Pipo, 7 Nov 1947, Schwarz 5144 (CTES). BRAZIL. 1876, Burchell 6876 (US); Maracuju, territory of Ponta Rosa, 1 Jun 1946, Swallen 9368 (US); MATO GROSSO: Mun. Rio Brilhante, 23 Oct 1970, Renvoize 972 (NY, US); PARANA: Guarapuava, 20-23 Mar 1946, Swallen 8862 (US): Lapa, 18 Feb 1946, Swallen 8617 (US); Mun. Laranjeiras do Sul, Km. 127, 12 Feb 1969, Hatschback 21126 (MO); Mun Palmas, 24 km NW of Palmas, 4 Dec 1971, Smith et al. 15650 (F, NY); Mun. Palmas, Rio Chopim, 4 Dec 1971, Hatschback et al. 28220 (NY); RIO GRANDE DO SUL: Morro Santa Teresa, 5 Sep 1949, Rambo 43713 (WIS); Mun. Bom Jesus, Feb 1902, Dutra 460 (US); Mun. Rio Pardo, Dec 1905, Jurgens G-170 (US); SANTA CATARINA: 17 km NE of the Santa Catarina-Rio Grande do Sul border, 11 Mar 1976, Davidse et al. 11144 (MO, NY); Mun. Abelardo Luz, 8-12 km N of Abelardo Luz, 15 Nov 1964, Smith & Klein 13330 (US); Mun. Lages, 4 Jan 1946, Swallen 8141 (US); SAO PAULO: Near S. Paulo, 22 Mar 1898, Edwall 2922 (US); inter Pilar et Alto da Serra prope Santos, 1902, Wacket s.n. (W); Fazenda Campo Grande, 30 Oct 1939, Viegas 5185 (US); Mun. Moji-Guacu, Fazenda Campininha, 3-3.2 km NNW de padua Sales, 20 Sep 1960, Mattos et al. 8242 (MO. US). PARAGUAY. In regione calcarea cursus superioris fluminis Apa, 1912-1913, Hassler 11075 (US); Caacupe, Barrerito, 21 Sep 1951, Burkart 18878 (US); Caaguazu, 11 Nov 1874, Balansa 2308b (W); Colonia Nueva Germania, Dec 1916, Rojas 10513a (SI, US); Tebicuary, Nov 1941, Rojas 9262a (US); between Villa Rica and Escoba, Jan 1889, Morong 547 (NY); Dtto. Misiones, Estancia "La Soledad", Santiago, 23 Sep 1959, Pedersen 5203 (NY). URUGUAY. RIVERA: Cerro Aurora, 10-15 Feb 1961,

Rosengurtt B-8433 (US).

Sorghastrum viride is distinguished by having yellowish or yellow-greenish spikelets. This species has a strict, large inflorescence up to 40 cm. S. viride may be confused with S. pellitum. However, in general terms, the present species is the only one having yellow or yellow-greenish color of its spikelets, as well as a shining and glabrous second glume. On the other hand, S. pellitum has darker spikelets, as well as a pubescent second glume. In addition, I think that there is a hybrid population that has either pale or dark spikelets, but always with a second glume pubescent. In general terms, this hybrid population does not show yellow or yellow-greenish spikelets. However, because of the lack of more information to show the existence of these hybrids, these intermediate forms will be includes within the species Sorghastrum pellitum (all the forms have pubescent second glumes).

Sorghastrum viride is distributed in South America, in the countries of Argentina, Brazil, Paraguay and Uruguay (Fig. 69). It occurs mainly in highlands, at an altitude ranging from 500-2000 m.

Sorghastrum viride is well adapted to swamps, or edges of rivers. It is also well established in wet ground zones. However, in its western distribution limit, in Argentina, it may be present in savannas and rocky areas.

Sorghastrum viride flowers principally from October to February. However, some individuals may be flowering in March, spring and summer of the Southern Hemisphere. This species, along with S. pellitum are the only Sorghastrum species that do not flower in the autumn.

Sorghastrum viride is related to Sorghastrum pellitum. They share an overlapping distribution area, where probably they are intercrossing. Hackel (1889) and Pereira (1982), have already pointed out the existence of intermediate forms. Within this probable hybrid population, there is a whole gradation of forms representing at their very extremes both parental forms. However, S. viride seems to be better adapted to higher and wetter places than S. pellitum. Due to the fact, that there is no other information available to confirm or reject this speculation, the species Sorghastrum viride may include all those individuals showing a glabrous second glume. On the other hand Sorghastrum pellitum has a pubescent second glume.

Figure 68. Sorghastrum viride. A. Basal part, bar=5 cm. B. Inflorescence, bar=5 cm. C. Ventral view of the spikelet, bar=1 mm

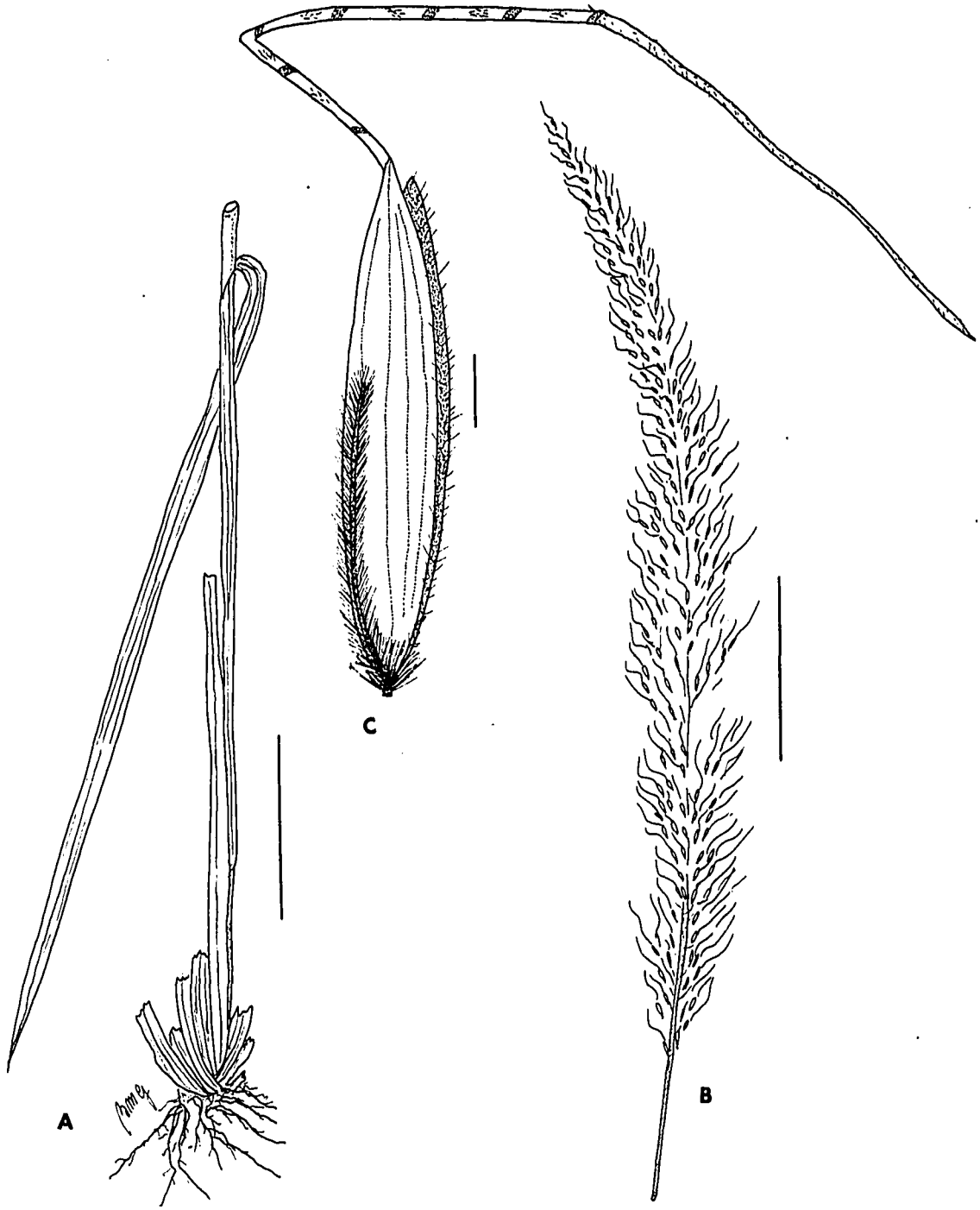
A
C
B

Figure 69. Distribution of Sorghastrum viride


S. viride
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X. SUMMARY

The first monographic work of the subtropical grass genus Sorghastrum is presented. Sorghastrum comprises 17 species inhabiting the New World and Africa. S. minarum, S. balansae, S. contractum, S. chaseae, S. pellitum, S. viride, S. scaberrimum, and S. stipoides are South American. S. rigidifolium and S. trichopus are African. S. incompletum and S. setosum inhabit Mexico, Central America and South America. S. brunneum occurs in Mexico and Central America. Finally S. secundum, S. elliottii, S. nudipes, and S. nutans are from North America.

The basic chromosome number of Sorghastrum is x=10. The dominant somatic number among Sorghastrum species is 2n=20. Of the 10 species with this number, five are form South America (S. scaberrimum, S. stipoides, S. pellitum, S. minarum, and S. viride), three are from North America (S. secundum, S. elliottii, and S. nudipes), the species S. brunneum occurs in Mexico; and S. setosum is distributed from Mexico to South America. On the other hand, four species have higher chromosome numbers than 2n=20. These are the two North American species, S. nutans with 2n=20,40, or 80, and S. incompletum var. incompletum with a somatic number of 2n=20 or 40, and two African species S. trichopus with 2n=40 and S. rigidifolium with a somatic number of 2n=40 or 60. Higher numbers in the African and North American species are consistent with a hypothesis of a South American origin of the genus.

In addition, a comparison of the basic and commonest somatic numbers of Sorghastrum to some related genera, such as Sorghum, Bothriochloa,

Andropogon, Dichanthium, Hyparrhenia, and Cleistachne was carried out. With the exception of Cleistachne the somatic number of these genera support the hypothesis of the Andropogoneae having a basic number of x=5.

Sorghastrum species seem to be cross-pollinated. In addition, from indirect evidence, there is a possibility that hybridization in Sorghastrum has taken place. With respect to the phenology of the genus, except for S. pelitum and S. viride which flower in the spring, the rest of Sorghastrum species flower during the autumn. The species of Sorghastrum may inhabit any of three different habitats. First, a savanna-like vegetation (mainly in South America. Second, pine-oak forests or woodlands (mainly in North America and Africa). Finally, swampy or boggy places (in Africa and the Americas).

Leaf cross sections, epidermal peels, and SEM epidermal studies proved to be important taxonomic tools in the study of Sorghastrum. With respect to leaf cross sections, some important points in defining Sorghastrum species are the following. The outline of the lamina may be open or inrolled. The midrib is mainly compound (formed by more than one vascular bundles), however, S. minarum and S. rigidifolium show a simple midrib (formed by only one first order vascular bundle), without association of parenchyma cells. There are three types of vascular bundles, i.e., first, second, and third order vascular bundles. Sorghastrum shows a single vascular bundle sheath. These sheaths are completely surrounding the second and third order vascular bundles, but they are abaxially interrupted by sclerenchyma in the first order

vascular bundles. Finally, bulliform cells are always present in the adaxial surface of the leaf. They may be generally fan-shaped, but occasionally form restricted groups of large, parallel-sided cells.

To examine the leaf epidermis, two different techniques were used (light and scanning electron microscopy). Some important points in defining Sorghastrum species are the following. The subsidiary cells of the stomata have a typical triangular form. The interstomatal cells may be either rectangular or square. Papillae are usually present; however, in S. balansae they are absent. Two different shapes of papillae are observed, globose and not overarching the stomata, or elongated and overarching the stomata. The shape of the intercostal short cells may be rounded, tall and narrow, or even square. On the other hand, the costal short cells may be rectangular or square. The silica bodies are typically dumbbell-shaped, usually the middle is narrow and short, but in S. elliottii and S. trichopus the silica bodies have a narrow long middle. Finally, the size of the prickles in Sorghastrum species may be small (smaller than the stomata), medium (the base slightly longer than the stomata), and large (base at least twice as long as the stomata).

In relation to the gross morphology survey, some useful features to be pointed out are the following. The rhizomes may be well developed or lacking. The culm may be caespitose, erect, nodding or clambering. The leaves may be expanded, inrolled or folded. Also, they may be pubescent on one or both surfaces, or glabrous. The ligule is membranous, glabrous or pubescent. In addition, it may be truncate or forming well developed auricles. With respect to the inflorescence, it is always represented by

a terminal panicle of rames. This panicle may be equilateral or secund. Also, it may be erect or nodding. the rachis is disarticulating at the base of the sessile spikelet. The sessile spikelet is always dorsally compressed, lanceolate, oblong or linear-oblong, dark or pale. Two florets are always present at the sessile spikelet, the lower reduced to a lemma, the upper perfect. The glumes are indurate and coriaceous, whereas the remainding bracts are hyaline. From the sinus of the fertile lemma, an awn is originating. The awn may be straight and non-twisted, or once or twice geniculate and twisted. Three stamens with the filaments reduced and the anthers well developed are present. Finally, a glabrous ovary and an ellipsoid caryopsis are present.

A complete survey of the nomenclatural status of the genus and its species was carried out. Based on typification rules, type specimens, and original descriptions, 17 species are accepted as legitimate. S. balansae represents a new combination proposed in this work. The species S. incompletum is defined in this dissertation as having two varieties (S. incompletum var. incompletum and S. incompletum var. bipennatum). In addition, a list of about 100 synonyms is listed. Generic and specific descriptions are given. In addition, an idetification key to the species of Sorghastrum was constructed. This key is mainly based on gross morphology characters.

A cladistic analysis for estimating the phylogeny of the genus Sorghastrum and its species was carried out. In relation to the phylogenetic estimation of the genus Sorghastrum, 11 characters were

polarized. It was compared with recognized related genera, such as Sorghum, Cleistachne, Dichanthium, Bothriochloa, and Andropogon. Two principal clades were observed. The first one is formed by Sorghum, Sorghastrum, and Cleistachne. The two latter genera, are sister groups, whereas Sorghum probably represents part of the ancestral genomic stock from which Sorghastrum originated. On the other hand, Cleistachne represents a more advanced taxonomic entity than Sorghastrum, but probably originating from it. The second clade is represented by Dichanthium and Andropogon. With the available data, there is not any key to recognize a recent phylogenetic association between Bothriochloa and the remainding genera.

With respect to the phylogeny of the species of the genus Sorghastrum, 22 characters were polarized. Three main clades were observed. Within the first clade, a first group is formed by S. minarum and S. balansae. These species are considered the most primitive within the genus. A second group of the first clade, is represented by S. pellitum and S. viride. These two species along with S. stipoides and S. scaberrimum are probably more closely related to one another than to the rest of the species of the first clade. Still within the first clade, the third group is formed by S. chaseae and S. incompletum. It seems that from a S. chaseae stock, a diverging line emerged giving rise to a successful annual species (S. incompletum) that invaded mainly Central America and Mexico. S. stipoides, S. scaberrimum, S. rigidifolium, and S. contractum belong to the first clade. They do not seem to share, with the available data, any derived state.

The second clade is formed by S. setosum and S. trichopus. It is a very specialized and defined set that is successfully established in swampy or boggy places.

The third clade is formed by five mainly North American species. Within this clade, two groups can be distinguished. The first one, is formed by S. elliottii, S. brunneum, and S. secundum. The first two species are closer to each other than to S. secundum. Possibly S. brunneum-like stock was the genetic source that eventually originated the species S. elliottii and S. secundum. S. elliottii originated from an evolutionary line recently diverged, whereas S. setosum comes from an evolutionary line that emerged earlier. The second group of the third clade is formed by S. nutans and S. nudipes. The former is a widespread species that probably represents the linkage with the South American genome stock. On the other hand, S. nudipes seems a recent evolutionary line emerging from S. nutans.

Finally, some preliminary biogeographic considerations are achieved in this work. Migration, long-distance dispersal or even land mass-movements may be involved in the explanation of the disjunct distribution of Sorghastrum. Lack of a fossil record, as well as comparative information of other related taxa make it impossible to completely explain the present distribution of Sorghastrum species. The general and preliminary considerations attempted in this work are the following. First, Sorghastrum probably originated from a Sorghum-like stock in the present Eastern South America and/or Western Africa. Second, a further

migration and specific radiation of Sorghastrum in South America, originated new South American species. Third, some related species showing disjunct distribution. i. e., S. setosum and S. trichopus represent a sample of the close relationship between South American and African Floras. Fourth and last, a more recent group of species is the North American one, probably originating from an ancestral South American stock.

XI. LITERATURE CITED

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XIII. APPENDIX

A. Doubtful Species

1. Sorghastrum tisserantii Clayton, Kew Bull. 30 (3):509. 1975. Clayton suggested this new species. The holotype (Tisserant s. n.) is from the Central African Republic, in Africa. Unfortunately this specimen is poor, so that both vegetative and floral characteristics are not clear. I think that probably it is a specimen of Sorghastrum minarum, but until more specimens are seen no more conclusions can be made.

B. Invalid Species

1. Sorghum trichocladum (Ruprecht) Kuntze, Rev. Gen Pl. 2:792. 1891. This taxon has been related to both Sorghum and Sorghastrum. However, with the information available it is clear that Sorghum trichocladum is not a Sorghastrum species, nor does it belong to section Sorghum of Sorghum. Further studies are needed to clarify its generic relationship

2. Sorghastrum baileyi Muell. Nomen nudum. The validity of this species is not accepted in this work. I have seen 4 US specimens, all from the Phillipines (Merill 593, 5360 and Ramos & Edano 43973, 44410) filed under Sorghastrum baileyi. All of them do not show the sterile pedicel typical of Sorghastrum. Therefore, I think that these specimens fit better within the genus Cleistachne.